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MOTOR AREAS AND SUPERFICIAL MUSCLE ACTION IN SALAMANDERS

By Theodore H. Eaton, Jr.

East Carolina College, Greenville, North Carolina

Preliminary experiments showed that it was possible to obtain sharply localized muscle action in salamanders anesthetized by chloretone, using pin-point electrodes, alternating current and a variable transformer. Since chloretone abolishes the reflexes of skeletal muscle, these movements were the result of direct stimulation through the skin. The electrodes could be used at a minimum distance of one millimeter apart, and in most cases a muscle so stimulated showed its prime action clearly, without involving others near it. Thus it became possible to map the several areas on the surface within which different actions were evoked. The term "motor areas" is used for these, by analogy with the motor points at which electrical stimulation causes localized muscle contraction in man; the latter, of course, correspond to the points at which motor nerves enter their respective muscles, but this discrimination cannot be obtained in animals of the size of salamanders.

The present study is part of a research program aided by a grant-in-aid from the National Science Foundation, administered through the Highlands Biological Station, Highlands, N. C. The writer is indebted to Miss Thelma Howell, Executive Director of the Station, for the use of laboratory and field facilities.

Adults of four species of Caudata were used, all locally available; one, *Triturus viridescens*, is a member of the Salamandridae, and the others, *Desmognathus quadramaculatus*, *Plethodon shermani rabunensis*, and *Aneides aeneus*, belong to the lungless Plethodontidae. The superficial muscles of *D. quadramaculatus* are shown in figure 1. They have not previously been illustrated, except for a part of the hyobranchial region (Piatt, 1935). The names used are, with two or three exceptions, those given by Francis (1934) for *Salamandra*, to which *Desmognathus* is quite similar in most features. The deeper muscles, and details of attachment and innervation, have not been concerned in the present work, nor has a dissection of the other three kinds been made. Therefore figure 1 serves simply as a guide in the following discussion. But the results show certain actions to be rather different from what various writers have stated by inference from the positions of muscles in dissected specimens. It is hoped that this study may lead to more careful interpretation of the prime action of muscles, which is necessary in establishing a comparative basis for kinesiology.

First it is important to note the limitations and possible sources of error in

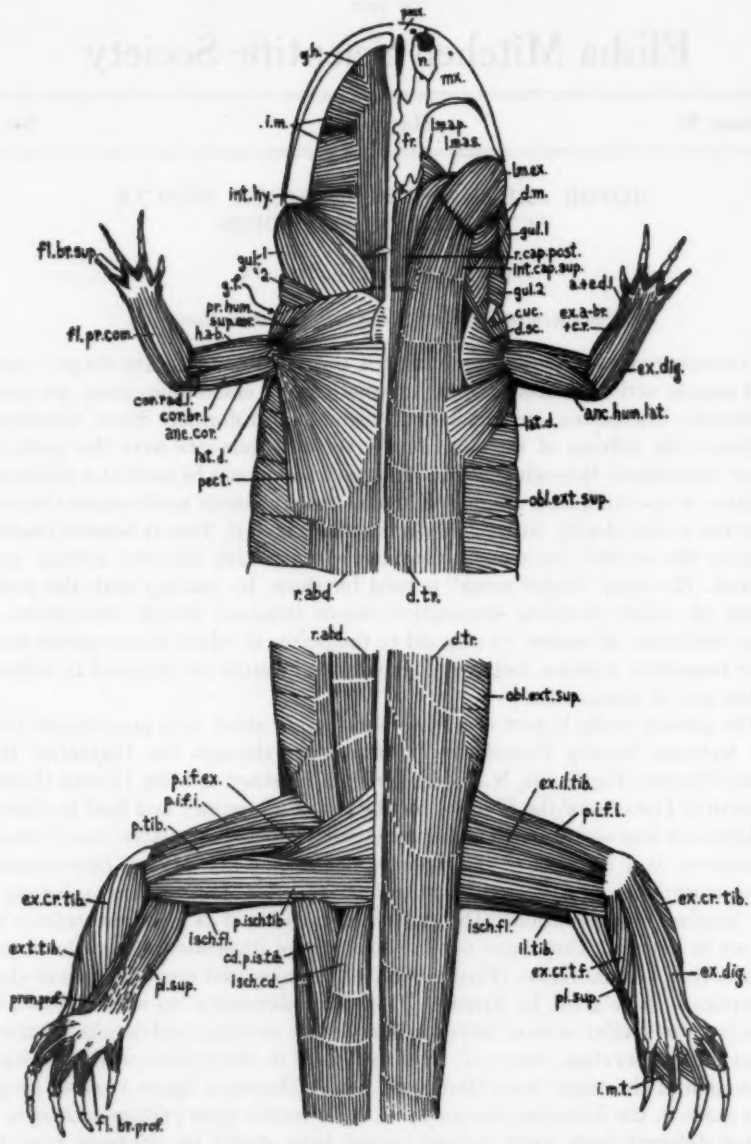

FIG. 1. Superficial muscles of *Desmognathus quadramaculatus* (adult, 108 mm.). In each illustration the left half is the ventral aspect, the right half the dorsal aspect. *a.* + *e.d.l*, m. abductor et extensor digiti primi; *anc.cor.*, anconeus coracoideus; *anc.hum.lat.*, anconeus humeralis lateralis; *cd.p.is.tib.*, caudali-pubo-ischio-tibialis; *cor.br.l.*, coraco-brachialis longus; *cor.rad.l.*, long tendon of coraco-radialis proprius; *cuc.*, cucullaris; *d.m.*, depressor

the method used. Chloretone anesthesia offers the great advantage that dermal stimulation will not result in reflexes, which may confuse and obscure the simple action being investigated. But the animal must not lie too long in the chloretone solution, or the responsiveness of the muscles dies away altogether. The heart, of course, is not affected at first, and the salamander may be removed from the chloretone and placed on a wet paper towel under the low power binocular as soon as it becomes insensitive to ordinary handling. Its skin cannot be allowed to dry, since it will then not conduct the current supplied by the electrodes. Fine electrode points were obtained by using *no. 3* insect pins and scraping the lacquer from their tips, but a position closer than about one millimeter is not practical since they may then frequently touch each other and short-circuit, or become fouled by mucus from the skin glands every time they touch the surface (mucus secretion inevitably accompanies the stimulation). Since the skin may reach nearly a millimeter in thickness, and since there are varying amounts of connective tissue beneath it, one cannot be certain that the regional limitations of a given motor area correspond precisely with the shape of a muscle under it; the motor area is dermal, and the muscle related to it is often only in partial contact with the skin. In certain cases it is impossible, even by reducing the current to a minimum, to distinguish two separate muscles from one another, for if they overlap and the superficial one is thin, both may respond to the same stimulus. Frequently it is necessary to take particular care that the moving part being studied shall be released from contact with the substratum or even from such a delicate obstruction as the surface film of water over it, for a weak muscle may not appear to act at all if it has any hindrance. Thus the effects of epaxial or lateral abdominal muscles can be seen best when the animal is suspended freely from the head. The weight of a limb, in the same way, may interfere somewhat with interpretation of the direction in which it is moved, unless it is suspended in a vertical position from the body. Finally, it is seldom that a given movement can be described correctly in a single word, such as flex or adduct; the exact direction may depend upon the point being stimulated, which means that for a broad muscle this method may not cause it to twitch as a whole.

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mandibulae; *d.sc.*, dorsalis scapulae; *d.tr.*, dorsalis trunci; *ex.a-br.* + *c.r.*, extensor antebrachii et carpi radialis; *ex.cr.t.f.*, extensor cruris et tarsi fibularis; *ex.cr.tib.*, extensor cruris tibialis; *ex.dig.*, extensor digitorum communis; *ex.il.tib.*, extensor iliotibialis; *ex.t.tib.*, extensor tarsi tibialis; *fl.br.sup.*, flexores breves superficiales; *fl.br.prof.*, flexores breve profundi; *fl.pr.com.*, flexor primordialis communis; *fr.*, frontal; *g.f.*, location of gular fold; *g.h.*, geniohyoideus; *gul.1*, deeper division of gularis (quadrato-pectoralis); *gul.2*, dermal division of gularis; *h.a-b.*, humero-antebrachialis; *il.tib.*, ilio-tibialis; *i.m.*, intermandibularis; *i.m.t.*, intermetatarsales; *int.cap.sup.*, intertransversarius capitis superior; *int.hy.*, interhyoideus; *isch.cd.*, ischio-caudalis; *isch.fl.*, ischio-flexorius; *lat.d.*, latissimus dorsi; *l.m.a.p.*, levator mandibulae anterior profundus; *l.m.a.s.*, levator mandibulae anterior superficialis; *l.m.ex.*, levator mandibulae externus; *mx.*, maxillary; *n.*, nasal; *obl.ext.sup.*, obliquus externus superficialis; *p.*, parietal; *pect.*, pectoralis; *p.i.f.ex.*, pubo-ischio-femoralis externus; *p.i.f.i.*, pubo-ischio-femoralis internus; *p.isch.tib.*, pubo-ischio-tibialis; *pl.sup.*, plantaris superficialis; *pmx.*, premaxillary; *pr.hum.*, procoraco-humeralis; *pron.-prof.*, pronator profundus; *r.abd.*, rectus abdominis; *r.cap.post.*, rectus capitis posterior; *sup.cor.*, supracoracoideus.

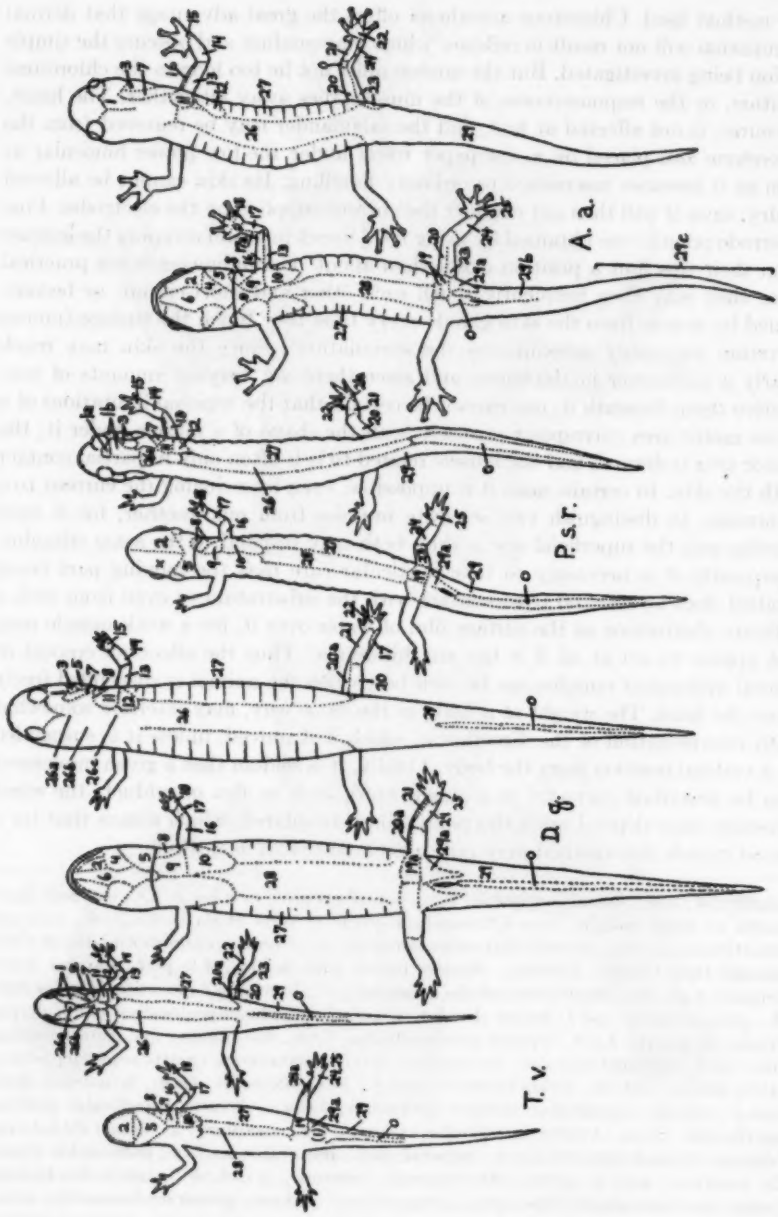

FIG. 2

The dotted lines in figure 2 indicate motor areas, in each of which a particular, discrete muscle action may be elicited by stimulation of the skin by the electrodes. The numbers used are intended to distinguish all the recognizable areas in each salamander, and to apply to comparable areas in the four species. It has not been possible to make them correspond exactly, because of probable differences in the muscles themselves, and because of some of the circumstances mentioned in the preceding paragraph. The differences in relative size of the specimens shown are as indicated in the drawings.

RESULTS AND DISCUSSION

1. The *levator mandibulae* and its divisions are essentially the same in *Desmognathus* as they are described in *Salamandra* by Francis (1934). The *l. m. externus*, however, originates in part from a raphe rising above the otic region and separating it from the anterior end of the *intertransversarius capitis superior*, so that the two seem like a continuous muscle. Just medial to this is the narrow, curved, and partly tendinous *l. m. anterior superficialis*, which takes origin from the dorsolateral corner of a collar-like ridge on the atlas vertebra; it runs, without further attachment, through a groove over the otic region and down to the coronoid process of the prearticular on the mandible. Over this region of the head, then, there is simple adduction of the mandible, but this effect blends into that of elevation of the head at the occipital joint as stimulation is brought farther back. The point of most abrupt elevation is at 26a, where it is caused partly by *rectus capitis posterior* and partly by *l.m.a.s.* It is necessary to emphasize that this mechanism is not different from that in *Salamandra* or in the other three forms investigated, for Dunn (1926, p. 45) indicated that it was: "The atlas slip of the *Temporalis* is tendinous in *Desmognathus* and *Leurognathus*. Thus the lower jaw is immovably attached to the atlas, and the mouth is opened by raising the skull. The function of this arrangement, with which is connected the stalked condyles, and collared atlas of these forms, is to prevent the downward bending of the head, and to stiffen the anterior part of the body." The stalked condyles and collared atlas are distinctive in these genera, simply increasing the leverage by which the *r.c.p.* and *l.m.a.s.* elevate the head, but the lower jaw is by no means immovably anchored to the atlas, the muscle which connects them is only in part tendinous, the mouth is not opened by raising the

FIG. 2. Motor areas of ventral (left) and dorsal (right) surfaces of four salamanders. *T.v., Triturus viridescens; D.q., Desmognathus quadramaculatus; P.s.r., Plethodon shermani rabunensis; A.a., Aneides aeneus.* 1, adductors of mandible; 2, intermandibularis; 3, depressor of mandible; 4, interhyoideus; 5, gularis; 6, geniohydoieus; 7, cucullaris; 8, procoracohumeralis; 9, supracoracoideus; 10, pectoralis; 11, dorsalis scapulae; 12, latissimus dorsi; 13, anconeus (upper arm extensors); 14, lower arm extensors; 15, extensors of digits; 16, upper arm flexors; 17, lower arm flexors; 18, flexors and adductors of digits; 19, adductors of femur; 20, upper leg extensors; 21, lower leg extensors; 22, foot and digit extensors and adductors; 23, upper leg flexors and adductors; 24, lower leg flexors; 25, foot and digit flexors and adductors; 26, epaxial trunk muscles; 27, lateral abdominal muscles; 28, rectus abdominis; 29, caudal flexors; 0, areas of no response.

skull, and the head can very easily be bent downward (cf. *gularis*). I gave particular attention to this mechanism, and found that it was wholly impossible to open the mouth by stimulation of the muscles which elevate the head; in fact it is opened in the same way as in other amphibians, by means of the *depressor mandibulae* (3), which has two slips.

In *Triturus* there is a fronto-squamosal arch, a primitive feature lost in most Caudata; the motor area is below this in *l. m. externus*, but above it in the other divisions. In *Plethodon*, and less distinctly in *Aneides*, stimulation of the area medial to the eye caused protraction of the mandible (*l. m. a. profundus*). Elevation of the head, as well as adduction of the mandible, was elicited from the more dorsal portions of *l. m.*

2. Action of the *intermandibularis* was shown by a lateral pulling of the skin of the throat, toward the point being stimulated. Since the *i.-m.* in *Desmognathus* and *Aneides* does not cross the whole throat, its motor area is easily distinguished laterally, but in *Triturus* and *Plethodon* the effect was noted as far as the midline, and it was difficult to distinguish it from that of the similarly placed *interhyoideus*. Stimulation at the point marked X in *Plethodon* caused partial tongue protraction, by the *subarcualis rectus 1*; this effect was also noted in the other salamanders, but less strongly.

3. The *depressor mandibulae* has two slips in *Desmognathus*, one originating on the posterior margin of the squamosal, the other on the lateral fascia over the *cucullaris*. Although the action is to depress the mandible, the motor area in which this may be elicited varies in the different species because the lower portion of the *d.m.* is more or less concealed under the *gularis*. In *Desmognathus* and *Aneides* only a small spot above the edge of the latter would give depressor action.

4. *Interhyoideus*. Action as described for *intermandibularis*. Both of these muscles must be active in the rhythmic elevation of the floor of the mouth which these salamanders employ in their oral breathing.

5. *Gularis*. This muscle is the *gularis* of Smith (1920) and Eaton (1937); *quadrato-pectoralis* of Drüner (1901) and Piatt (1935); *interhyoideus posterior* of Francis (1934). In most salamanders the *gularis* is attached to the quadrate anteriorly and to the skin of the gular fold ventrally; the former is always stated to be the origin, the latter the insertion. In *Desmognathus* and in *Aneides* (cf. Piatt, 1935) there is also a wholly dermal derivative of it, reaching from the gular fold to the skin of the cheek (Fig. 1, *gul. 2*), which can be seen to draw the latter downward slightly. The major part of the muscle (*gul. 1*) has an important action as depressor of the head as a whole; this effect can be produced in *Triturus* and *Plethodon* by stimulation at the midline, and in the others by simultaneous stimulation of the two sides, since the muscles are separated medially. Unilateral stimulation twists the head downward and to one side. The skin of the gular fold therefore serves as the origin, for it is only slightly moved, while the quadrate must be regarded as the insertion. The *gularis* is particularly large and powerful in *Desmognathus*, and is responsible for the swollen sides of the neck as well as the deflected position of the head often seen in preserved salamanders of this genus.

6. The motor area for the *geniohyoideus* is the middle third of the throat, but the muscles just described (*2*, *4*, *5*) may interfere in some cases with observation of its action. In salamanders generally it runs as a pair of straps from the symphysis of the mandible to the second basibranchial (urobranchial, or os triangulare), which is the only ossified part of the hyobranchial skeleton in most Plethodontidae. The action is to draw the latter forward, rather than to depress the mandible; this is true even when the mandible has been released from contact with the upper jaw and has no hindrance whatever to its downward movement. Therefore it would be proper to regard the mandible as the origin.

7. The *cucullaris* turns the head laterad, and at the same time draws the pectoral girdle slightly forward. Its motor area, however, is often partly obscured by overlapping of other muscles. In *Aneides* it is shown as a long, narrow zone, but undoubtedly the more anterior part of this is actually in the motor area for the *intertransversarius capitis superior*, which likewise produces a lateral flexion of the head, and the same must be true in *Desmognathus*.

8. The *procoracohumeralis* extends the humerus forward and slightly ventrad; its origin is partly covered by the gular fold and the *gularis* muscle, hence stimulation in this area will usually cause contraction of both muscles.

9. The *supracoracoideus* causes adduction of the humerus ventrally and medially, somewhat forward in the case of *Plethodon*, and in the others varying according to the section of the muscle stimulated.

10. The *pectoralis* causes postero-medial to medial ventral adduction.

11. The *dorsalis scapulae* elevates the humerus in the direction of the point stimulated.

12. The *latissimus dorsi* causes elevation and posterior adduction of the humerus.

13. The *anconeus* is the extensor of the ulna, its four divisions being inserted on the olecranon process, but in addition it indirectly flexes the humerus, for two of its heads (*a. coracoideus* and *a. scapularis*) originate from the pectoral girdle as indicated by their names. Stimulation of the posterior aspect of the arm causes the humerus to be drawn back toward the body, as well as extension of the ulna.

14. The effect of the *extensor digitorum communis* is to extend (or dorsiflex) the digits, and indirectly to dorsiflex the hand at the wrist. In addition the forearm is elevated when this area is stimulated in its proximal portion. In *Aneides* there is extension of the forearm as well as elevation, at the more posterior edge of the area. Also, in *Aneides*, extension of digits is obtained much more adequately from area *15*, scarcely at all from *14*. Along the anterior margin of *14* there is usually inward rotation of the hand, while on the posterior edge a slight outward rotation occurs.

15. Here there is both extension of the digits on the hand and adduction of the digits toward each other (*extensores breves digitorum* and *intermetacarpales* respectively).

16. The main effect on the ventral side of the upper arm is straight flexion of the forearm (*humero-antebrachialis*); this can be elicited a little way beyond the elbow in *Desmognathus*. In *Plethodon* I noted at the posterior border of *14* flexion

of forearm plus posterior adduction of upper arm (presumably the latter by *coraco-brachialis longus*).

17. The general effect here is palmar flexion, but in the proximal part of the forearm there is also depression of the forearm itself. Distally the digits become flexed as this zone merges with *18*. *Aneides aeneus* is a climber on rock ledges and under the bark of trees; its terminal phalanges are slightly broadened, giving the toes an increased pad for contact. But in the fore foot only the terminal phalanges of digits *2*, *3*, and *4* are flexed by stimulation in area *17*.

18. The digits are flexed when the palm is stimulated (*flexores breves superficiales*) and adducted when the bases of the digits are stimulated (*intermetacarpales*). In *Aneides* there is a zone of no response on the palm between *17* and *18*, and digit *1* can be adducted but not flexed.

19. Adduction of the femur is performed in more than one way. In *Triturus* area *19* produces ventral adduction, with a swing forward in the anterior part, and backward in the posterior; there is no apparent distinction between the area on the body and that on the ventral side of the thigh. Ventral flexion of the lower leg takes place with adduction of the femur. Essentially the same effect takes place in the other species, but in *Plethodon* and *Aneides* it was possible to distinguish an area on the body (*19*), with adduction of the femur, from that on the thigh (*23*), with both adduction of the femur and flexion of the lower leg. Area *29a* should be mentioned here because, although it contains ventral tail muscles, stimulation brought posterior adduction of the femur in *Desmognathus* and *Aneides*. (*Caudali-pubo-ischio-tibialis* is attached to the fascia covering the surface of *pubo-ischio-tibialis*.)

20. This is the area occupied by the extensors of the knee. Anterior to it is a zone in which the effect is forward flexion and slight elevation of the femur (*20a*), caused by the *pubo-ischio-femoralis internus*. The strongest elevation takes place when the stimulus is in the groove just over the base of the leg.

21. Two effects result from stimulation here: dorsiflexion of the foot and extension of the lower leg at the knee; this is because the origin of the *extensor digitorum communis* is from a fascia crossing the knee joint. The area marked *22* in the figure of *Triturus* should show *21* in its more proximal half. On the anterior edge of *21* there is produced an inward rotation of the foot, while a similar zone on the posterior edge causes a lateral or outward rotation.

22. In this area there is dorsiflexion of the foot without extension of the lower leg, and the digits are extended when stimulation is on the foot itself. (This does not include the first digit in *Aneides*.) At the bases of the digits they are made to adduct toward each other.

23. This has already been mentioned in connection with *19*; there is flexion of the lower leg plus indirect ventral adduction of the femur.

24. Here are produced both plantar flexion and the ventral flexion of the lower leg at the knee (*plantaris superficialis*). In *Aneides* there is also a partial inversion of the foot, its upper surface turning mediad and down; at the posterior edge it turns back.

25. Adduction and flexion of digits is obtained in this area, which may not be distinguished sharply from *24*. The first digit in *Aneides* will not flex.

26. The epaxial muscles of the trunk give local (3 or 4 segments) extension or dorsiflexion of the trunk when stimulated on both sides or near the middle line; more laterally they produce a lateral bend of the body. Posteriorly this motor area continues into that of the tail (*29*). Anteriorly, in the neck, there is differentiation in both structure and action. Stimulation from about the level of the scapula forward results in either elevation of the head (if medial or bilateral) or lateral bending of the head and neck; the extent of these responses is greater the farther forward is the stimulation. For instance, in *Desmognathus* stimulation at *26a* gives a sharp elevation of the head at the occipital joint, *26b* twists the head laterally, *26c* gives elevation of both head and neck. The strongest lateral flexion of the body is produced just anterior to the upper end of the ilium.

27. In *Triturus* the *obliquus externus* contracts locally, at the point of stimulation, forming a groove running antero-dorsally in the segment; thus the direction of this groove on the surface indicates the direction of the fibers. But in *Desmognathus*, where the fibers of the superficial layer run more nearly vertically and where (in a large specimen) the deeper ones are not affected, the result is a local wrinkling of the skin, in which several small folds run nearly horizontally but dipping slightly down and forward; these folds are at right angles to the muscle fibers. Essentially the same is seen in *Aneides*, but the contraction may include three or four segments. In *Plethodon* a whole segment (between two costal grooves) contracts at one stimulation, and there is lateral bending of the trunk.

28. Contraction of the *rectus abdominis* is local when weakly stimulated, resulting in wrinkling of the skin, but a strong stimulus will cause ventral flexion of the trunk (especially noted in *Triturus*). The Plethodontidae lack the ypsiloid cartilage at the posterior end of the abdomen, which is present in *Triturus*; stimulation immediately in front of the pelvis in the midline causes a deep pit to form, apparently by the upward (dorsal) lifting of the ypsiloid cartilage into the abdomen. Since this effect is produced by stimulus in the location of the *ypsiloideus posterior* (*pyramidalis*), which runs on each side from the pubis to the ypsiloid cartilage, it seems that this muscle is the elevator of the cartilage rather than its depressor, as stated by Francis (1934, p. 96).

29. Muscles of the tail tend to form a band along either side, in which the distinction between epaxial and hypaxial components is slight, and in the midline dorsally and ventrally there is a narrow zone in which no response to stimulation takes place. At the sides of the vent, however, there is differentiation into a more medial *ischio-caudalis* and a more lateral *caudali-pubo-ischio-tibialis*. In this region the effects are not entirely clear. In *Triturus* stimulation at *29a* causes a slight flexion of the tail, but mainly a puckering and forward movement of the cloaca lips, on which, however, no muscular response is induced. In *Desmognathus* and *Aneides* a postero-ventral adduction of the femur is produced in *29a*, as well as some flexion of the tail and a pulling of the pelvis slightly back-

ward. Only the latter two effects were noted in *Plethodon*. In most of area *29* in all of the salamanders there is lateral flexion of the tail, but *Aneides* is peculiarly specialized. In the more distal half of its tail (*29c*) stimulation of the sides produces lateral bending, on the dorsal side slight elevation, and on the ventral side a considerable downward thrust; these effects can be induced all the way to the tip. When walking up a vertical wooden surface the salamanders used approximately the last 20 mm. of their tails as a prop, not at every step, but frequently. The tail was bent sideways, its tip pressed against the surface, then straightened. I have seen similar action in *Hydromantes brunus*, carried out with more vigor and synchronized with the hind legs (cf. Gorman, 1954); it is likewise reported for *H. shastae* (Gorman and Camp, 1953), *H. platycephalus* (Stebbins, 1947), *Pseudoeurycea cephalica rubrimembris* and *P. galaenae* (Taylor and Smith, 1945). Smith (1947) has commented upon the mechanism, and regards it as of independent origin in *Hydromantes* and *Pseudoeurycea*.

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A STUDY OF THE BRYOZOA OF BEAUFORT, NORTH CAROLINA, AND VICINITY[1]

By Frank J. S. Maturo, Jr.

Department of Zoology, Duke University, Durham, N. C. and Duke Marine Laboratory, Beaufort, N. C.

Among the host of invertebrates which make up the fouling complex in the sea, the Bryozoa are probably second only to hydroids in the number of species involved. Experiments in recent years have revealed this group as one of the most conspicuous and prevalent components of test surface populations. Yet conspicuous gaps in the recorded distribution of many species occur for want of sufficient faunistic studies. Along the Atlantic coast of North America almost nothing is known about these animals from Chesapeake Bay to the southern tip of Florida and the West Indies.

In view of the lack of information on this group the present study was undertaken to discover what bryozoans occur in the vicinity of Beaufort, North Carolina, how they are locally distributed, and their substrate preferences. A subsequent report will consider their temporal or seasonal distribution, spatial distribution, reproductive periods and rates, and the role of environmental factors as related to these.

General description of the Beaufort area.—The Beaufort area has figured prominently in marine biological studies during the last fifty years as a result of the investigations at three marine laboratories there. The suitability of the region for such studies becomes obvious when one considers the wealth of fauna and flora available because of its geographical location and topography. It has been found by numerous workers that the region, which is intermediate between Woods Hole and Florida, is the southern limit along the Atlantic coast for many northern forms and the northern limit for a host of southern species.

Historically, the Beaufort region includes not only the immediate inshore areas around Beaufort, North Carolina, but also waters offshore to the Gulf Stream, east to Cape Lookout, and west or southwest to New River Inlet or to Cape Fear. The coast follows a general east-west direction with the Gulf Stream lying about thirty miles offshore. The coastline is separated by offshore islands or outer banks from the ocean proper so that numerous sounds and estuaries are inclosed. The bar-built estuaries and sounds are considered somewhat positive, that is, they possess a measurable dilution of sea water by river water, the mixing primarily a result of tidal action coupled with a large effect of wind in shallow water. The bottom is composed of mud, sand, and shells, varying from place to place, and extensive marshes, shoals, and oyster reefs are scattered throughout the area. The man-made rock jetties and harbor works, in addition to the shell bottoms, afford excellent habitats for Bryozoa.

About 21 miles offshore in 13 to 15 fathoms of water is an extensive series of reefs or "fishing banks." The main bank, as reported by Radcliffe (1914) from

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a survey conducted by the U. S. Fisheries Steamer *Fish Hawk*, lies in Lat. 34° 19′ N., Long. 76° 59′ W., and is the largest reef known on the coast. The fauna and flora of these reefs which have been reported from a few meager collections are tropical forms, much the same as in the West Indies. Between the "fishing banks" and the outer banks is a veritable desert as far as bryozoans are concerned, because the bottom type is only sand, and offers no suitable substrate. However, great masses of seaweed which support a bryozoan fauna are found in this area, carried there by currents from the "fishing banks" and other regions.

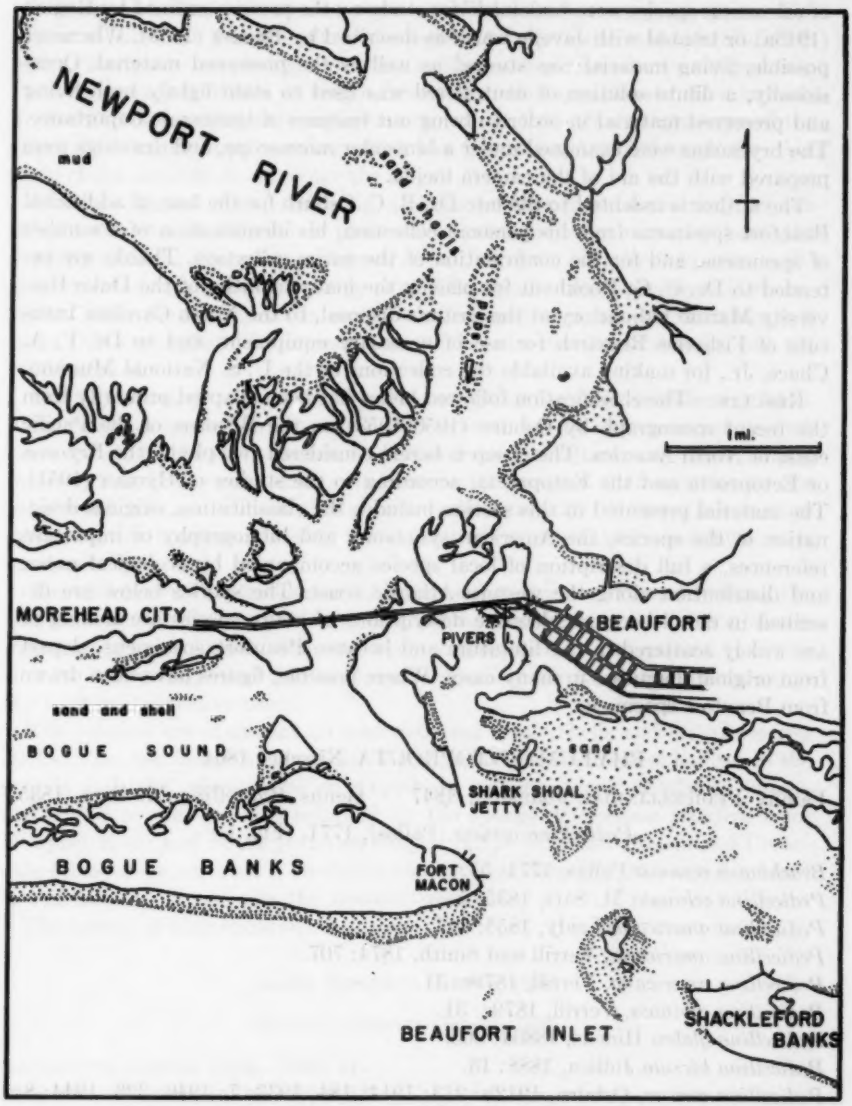
Thorough reports on the environmental conditions at Beaufort may be found in papers by Hoyt (1920), Gutsell (1930), McDougall (1943), and others.

Bryozoan studies on the Atlantic Coast.—Perhaps no area on our Atlantic coast has been studied as thoroughly as the Woods Hole region. Osburn (1912b) has done the major part of the work there and has reviewed studies on Bryozoa of the Atlantic coast up to that time. Later, Osburn (1933) made a survey of the bryozoans of Mount Desert Island, Maine. Rogick has been responsible for most new records from Woods Hole. The works of Hutchins (1945) on Long Island Sound, and Osburn (1932b, 1944) at Chesapeake Bay, complete studies on Bryozoa to the north of Beaufort.

Smitt (1872–1873) prepared the earliest important work in the Florida region, his studies being confined primarily to deep water forms. Osburn reported on the bryozoans of the Tortugas Islands (1914), Curacao and the southern Caribbean Sea (1927, 1947), and Puerto Rico (1940). Canu and Bassler (1928) reported the species found in the Gulf of Mexico region. Mention should also be made of a series of papers by Verrill from 1900 to 1902 on the fauna of Bermuda. Studies by Marcus since 1937 have contributed a wealth of information on species found in Brazilian waters.

In the Beaufort area, the first records of Bryozoa are those of 17 species reported by Verrill (1878) in a study of the natural history of Fort Macon, North Carolina, and vicinity, by Coues and Yarrow. Osburn has mentioned a number of species in the area at various times in his reports on other localities. Most of his specimens were collected on the "fishing banks." The seasonal study of McDougall (1943) lists eight species, while the faunistic report of Pearse and Williams (1951) records 24 species from reefs off New River Inlet, North Carolina.

METHODS AND MATERIALS.—An attempt was made to cover as many ecological situations as possible at various seasons over a two-year period. Bryozoan specimens were collected from shells, rocks, pilings, experimental racks, submerged debris, and algae which were found around Beaufort, and at Shackleford, Fort Macon, and Shark Shoal jetties and beaches (see map). Extensive dredgings in the various sounds and Newport River estuary as well as several dredgings and trawlings offshore were made. The most productive source of material was from shells dredged from Bogue Sound in front of Morehead City Port Terminal. A record book was kept in which each collection was catalogued together with habitat information, identifications, and memoranda on particular specimens.



Map of Beaufort, North Carolina, and vicinity, with notations on the bottom types.

Specimens were preserved in 70 per cent alcohol for study. In addition, samples of calcareous species were "calcined" for study by the process outlined by Rogick (1945a) or treated with Javelle water as described by Bassler (1953). Whenever possible, living material was studied as well as the preserved material. Occasionally, a dilute solution of neutral red was used to stain lightly both living and preserved material in order to bring out features of taxonomic importance. The bryozoans were examined under a binocular microscope, and drawings were prepared with the aid of the camera lucida.

The author is indebted to the late Dr. R. C. Osburn for the loan of additional Beaufort specimens from his personal collection, his identification of a number of specimens, and for the confirmation of the entire collection. Thanks are extended to Dr. C. G. Bookhout for placing the many facilities of the Duke University Marine Laboratory at the writer's disposal, to the North Carolina Institute of Fisheries Research for use of necessary equipment, and to Dr. F. A. Chace, Jr., for making available the collections of the U. S. National Museum.

RESULTS.—The classification followed below has been adapted primarily from the recent monograph by Osburn (1950–1953) on the Bryozoa of the Pacific coast of North America. The group is herein considered two phyla, the Bryozoa or Ectoprocta and the Entoprocta, according to the studies of Hyman (1951). The material presented in this section includes the classification, original designation of the species, the American synonomy and bibliography of important references, a full description of local species accompanied by ecological notes, and distribution along the western Atlantic coast. The species below are described in detail because adequate descriptions of many species are lacking or are widely scattered in the literature and because Beaufort specimens depart from original diagnoses in many cases. Where possible, figures have been drawn from Beaufort specimens.

PHYLUM ENTOPROCTA Nitsche, 1864

Family PEDICELLINIDAE Johnston, 1847 Genus *Pedicellina* M. Sars, 1835

Pedicellina cernua (Pallas), 1771. (Fig. 1.)

Brachionus cernuus Pallas, 1771: 57.
Pedicellina echinata M. Sars, 1835: 5.
Pedicellina americana Leidy, 1855: 143.
Pedicellina americana, Verrill and Smith, 1874: 707.
Pedicellina americana, Verrill, 1879c: 31.
Pedicellina echinata, Verrill, 1879c: 31.
Pedicellina glabra Hincks, 1880a: 565.
Pedicellina hirsuta Jullien, 1888: 13.
Pedicellina cernua, Osburn, 1912b: 213; 1914: 184; 1933: 7; 1940: 326; 1944: 8; 1947: 2.
Pedicellina cernua, Marcus, 1938: 5.
Pedicellina cernua, Rogick and Croasdale, 1949: 65.

The colony consists of small, soft-bodied, inconspicuous individuals (calyxes) which arise on flexible muscular stalks (pedicels) from a creeping stolon. The rather transparent stolon is divided irregularly into fertile and infertile internodes, the fertile ones being somewhat swollen and giving rise to the pedicels. Pedicels average 0.40 mm. in length, broadest at the base, about 0.07 mm. wide in Beaufort specimens, tapering gently to about 0.03 mm. at the base of the calyx. The longitudinal muscles which can be distinguished through the thin walls of the pedicels do not enter the calyx.

The cup-shaped calyx, distinctly gibbous (swollen asymmetrically) on one side, terminates distally in a transverse tentacular ring enclosing both the mouth and anus. The calyx measures about 0.25 mm. long by 0.15 mm. in diameter, which compares favorably with Chesapeake Bay specimens (Osburn, 1944). There are 8 tentacles in most Beaufort specimens, though the range is 8 to 24 (Marcus, 1939). The tentacles cannot be retracted into the calyx, but are rolled inward.

Short spines may or may not be present on either the calyx or pedicel or both. This variation has led to separation into several species by some workers, but since differences in the presence and distribution of spines may occur among the members of the same colony, it is currently accepted that only one species is involved. The spined condition of both pedicel and calyx is the rule in mature specimens in Beaufort material, while the buds and immature individuals are unarmed.

The members of living colonies move incessantly by arching and twisting the pedicel. Occasionally this process or injury results in the loss of the calyx, whereupon regeneration follows. Since the body wall is generally transparent, it is possible to observe algae and diatoms being rotated rapidly by ciliary action within the U-shaped digestive tract.

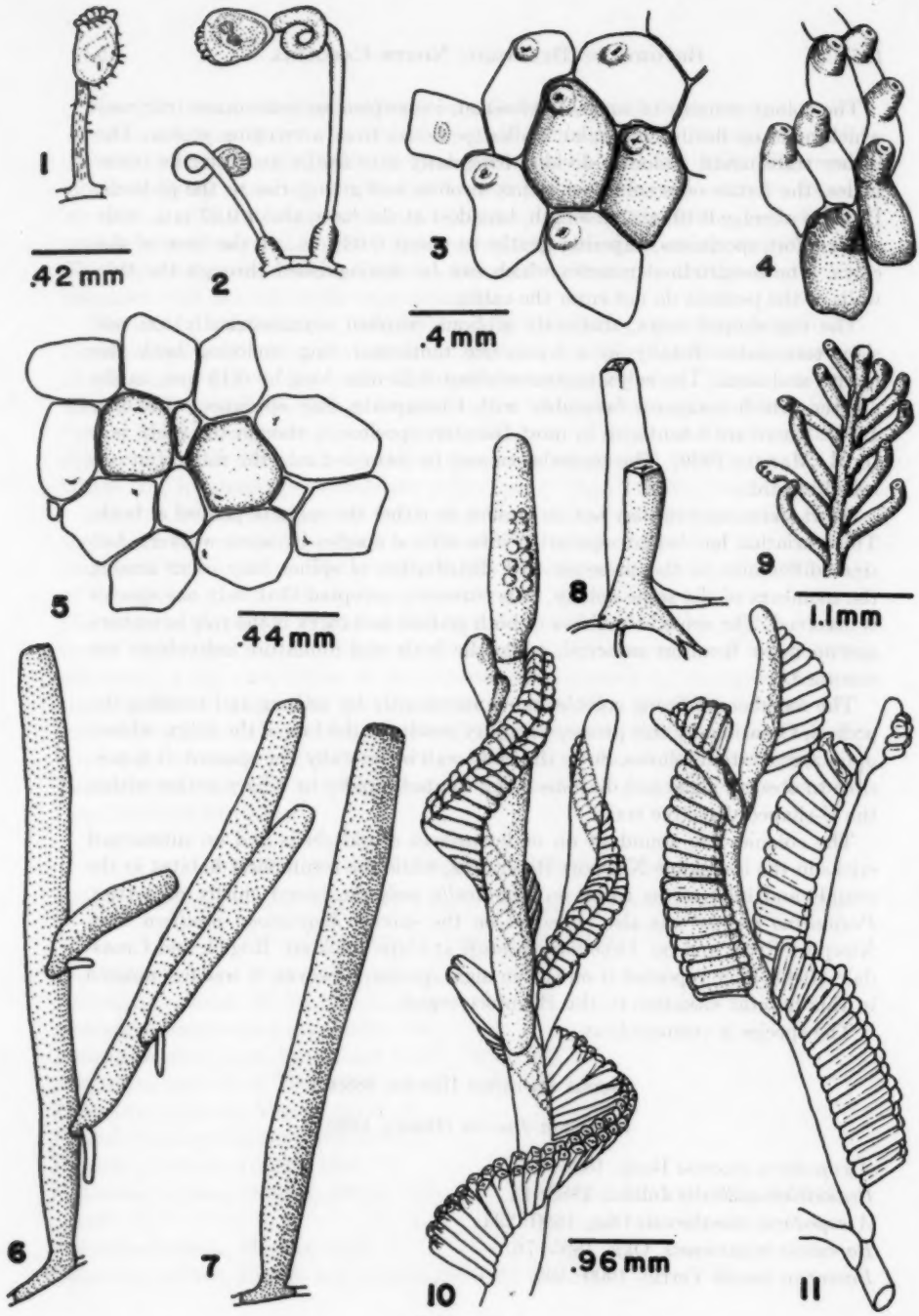
The colonies are abundant on undersurfaces of old shells and on submerged sticks in the less saline Newport River area, while the commonest habitat in the sounds and inlet seems to be on *Anguinella palmata*, found chiefly on jetties. *Pedicellina cernua* was also collected on the sponge *Microciona prolifera* from Newport River and on *Alcyonidium hauffi* at Cape Lookout. Rogick and Croasdale (1949) have reported it on eleven algal species; however, it was not noticed in this habitat situation in the Beaufort region.

The species is cosmopolitan.

Genus *Barentsia* Hincks, 1880

Barentsia discreta (Busk), 1886

Ascopodaria discreta Busk, 1886: 44.
Pedicellina australis Jullien, 1888: 13.
Ascopodaria misakiensis Oka, 1890: 234.
Barentsia misakiensis, Oka, 1895: 76.
Barentsia timida Verrill, 1900: 594.



FIGS. 1–11

Barentsia discreta, Osburn, 1912b: 214; 1914: 185; 1940: 327; 1944: 9; 1947: 3.
Barentsia discreta, Marcus, 1937: 15.

The colony is stolonate, the creeping stolon jointed at intervals where pedicels arise or where branching occurs. Members of a colony consist of an ovoid calyx bearing 16 to 20 tentacles and a rigid, chitinous, straw-colored pedicel which appears to be perforated by numerous funnel-shaped pores. Osburn (1944) observed that these pores are pits in an inner chitinous sheath and do not penetrate the outer layer of the pedicel, thus correcting Busk's description. The base of the pedicel is enlarged, barrel-shaped, and somewhat annulated. Individuals may reach a height of 4.4 mm. but are usually much smaller.

The species, though widely distributed throughout the world, was not found during the present survey, but was previously recorded by Osburn (1912b) for the Beaufort area.

Barentsia laxa Kirkpatrick, 1890. (Fig. 2.)

Barentsia laxa Kirkpatrick, 1890: 624.
Barentsia laxa, Marcus, 1938: 10.
Barentsia laxa, Osburn, 1944: 10.
Barentsia laxa, Rogick, 1948: 128.

This species can be distinguished from the preceding one by its thin-walled, flexible pedicel which possesses a septum, perforated by a central pore, just above its muscular, barrel-shaped base. Members of a colony usually arise in clusters from a creeping stolon, the basal expansions being separated by short infertile internodes. The individuals are among the largest of the entoprocts, reaching up to 9 mm. in height, though Beaufort specimens rarely exceed 4 mm.

The calyx is flattened on the anterior esophageal end and lightly gibbous on the posterior or intestinal end. The size is variable, depending on age; the average dimensions are 0.55 mm. long by 0.33 mm. wide. The internal organs can be readily distinguished through the transparent walls of the calyx. The tentacle number ranges from 13 to 23 (Rogick, 1948).

The pedicel varies considerably in length, the largest measuring 3.1 mm. It is finely annulated from the distal end to about three-fourths of the distance to the basal enlargement, and tapers gently to its narrowest point at the septum, where its average diameter is 0.04 mm. At its widest diameter just below the calyx it measures 0.07 mm. The upper portion of the pedicel appears to be the

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FIG. 1. *Pedicellina cernua* (Pallas), with tentacles rolled inward. FIG. 2. *Barentsia laxa* Kirkpatrick, with tentacles rolled inward. Note loop in the flexible pedicels; same scale as Fig. 1. FIG. 3. *Alcyonidium polyoum* (Hassall), with slightly puckered orifice. FIG. 4. *Alcyonidium mammillatum* Alder, showing mammillate condition of the orifice; same scale as Fig. 3. FIG. 5. *Alcyonidium hauffi* Marcus. Note that there is no oral prominence. FIG. 6. *Sundanella sibogae* (Harmer), showing method of branching; same scale as Fig. 5. FIG. 7. *Nolella stipata* Gosse, without a basal expansion; same scale as Fig. 5. FIG. 8. The same, with basal expansion; same scale as Fig. 5. FIG. 9. *Anguinella palmata* van Beneden. FIG. 10. *Amathia convoluta* Lamouroux. FIG. 11. ?*Amathia convoluta* Lamouroux; same scale as Fig. 10.

more flexible end, for here one or more loops may occur. The basal enlargements measure about 0.15 mm. in length and 0.1 mm. in width. Occasionally, a secondary basal expansion may occur some distance up the pedicel.

The colonies were found most abundantly on the upper surfaces of hard substrates in areas of lowered salinities such as Newport River and Beaufort harbor. This is the first report of the species from the Beaufort area, but it has been collected in the western Atlantic at Cape Cod, Chesapeake Bay, and Brazil.

PHYLUM BRYOZOA Ehrenberg, 1831

Class GYMNOLAEMATA Allman, 1856 Order CTENOSTOMATA Busk, 1852
Suborder CARNOSA Gray, 1841 Family ALCYONIDIIDAE Johnston, 1849

Genus *Alcyonidium* Lamouroux, 1812

Alcyonidium polyoum (Hassall), 1841. (Fig. 3.)

Sarcochitum polyoum Hassall, 1841: 484.
Alcyonidium mytili Dalyell, 1847: 36.
Alcyonidium rubrum Verrill, 1879b: 188.
Alcyonidium mytili, Osburn, 1912b: 251.
Alcyonidium polyoum, Osburn, 1933: 61; 1944: 15.
Alcyonidium polyoum, Marcus, 1937: 125.
Alcyonidium polyoum, Rogick and Croasdale, 1949: 45.

The zoarium forms a gelatinous crust which follows the contour of the substrate and is never erect. Zooecia are usually hexagonal, somewhat inflated, smooth surfaced, and separated by a distinct groove. The orifice is slightly puckered in the contracted state. The polypide is faintly visible through the frontal wall. The zooecia are 0.22–0.66 mm. long, 0.22–0.40 mm. wide, averaging 0.5 mm. and 0.4 mm. for length and width, respectively. These ranges are slightly greater than those reported by Rogick and Croasdale (1949: 47).

The color of Beaufort specimens varies from dull white to yellowish-brown, but occasional colonies have unicellular algae on them, which gives them a dark green color. A brick-red or red-orange form (Verrill's *A. rubrum*) which appears farther north has not been collected in this area.

The zoaria were found encrusting shells, pilings and rocks in Bogue Sound. One large specimen was collected from a shell inhabited by the hermit crab *Pagurus pollicaris*, the colony spreading over valves of living oysters and *Crepidula fornicata* attached to the shell and around the columella into the chamber occupied by the crab. Osburn has a local specimen taken from the legs of a spider crab (*Libinia*) and Pearse (1947) has found it on the blue crab *Callinectes sapidus*. Magalhaes (1948) reports the species as a very common consortes of the various species of *Busycon*. This species has been reported also on algal substrates.

Alcyonidium mammillatum Alder, 1857. (Fig. 4.)

Alcyonidium mammillatum Alder, 1857: 154.
Alcyonidium mamillatum, Osburn, 1919: 607; 1923: 6D; 1932a: 366; 1933: 62.
Alcyonidium mamillatum, Marcus, 1937: 126; 1939: 162.

The zoarium encrusts shells and occasionally hydroid stems. Zooecia are ovoid to elongate with the orifice situated on top of a stout oral prominence which is transversely wrinkled. They are about 0.6 mm. long by 0.22 to 0.4 mm. wide. The mammillate condition is characteristic and best seen if specimens are viewed in profile. The color is a yellowish-brown, depending somewhat on the color of the substrate since the colonies are quite thin. Tentacles number about 14.

Only one small colony was collected, found in the hinge teeth of a large *Venus* valve dredged from seven fathoms, just east of Beaufort Inlet (January 10, 1955). Osburn has taken a small specimen from "piles of harbor" (Beaufort).

The species is widely distributed in colder waters.

Alcyonidium verrilli Osburn, 1912

Alcyonidium ramosum Verrill, 1872: 289 (nec Lamouroux, 1824).
Alcyonidium ramosum, Verrill and Smith, 1874: 708.
Alcyonidium verrilli Osburn, 1912b: 252; 1944: 14.

"The zoarium, attached to stones, shells, and stems, is more or less cylindrical, sparsely branched and may reach a height of 100–350 mm. The color ranges from yellowish to dull brown. Rounded branches are usually between 5 mm. and 10 mm. in diameter, but flattened portions of the stem may be considerably larger. The zooecial walls are comparatively thick and the surface more or less level, but at the growing edges of the colony the surface may appear roughened by the slight protrusion of the transversely wrinkled tips of the zooecia" (Osburn, 1944).

The only record for this species in the Beaufort area is by McDougall (1943). It is quite possible and probable that the material examined was the following species, *Alcyonidium hauffi*, from which it differs in color, mode of growth, and the nature of the oral prominence. However, these differences at times may be quite subtle, particularly if the specimen is small and the oral prominence is fully constricted and retracted.

The distribution is from Chesapeake Bay to New England.

Alcyonidium hauffi Marcus, 1939. (Fig. 5.)

Alcyonidium hauffii Marcus, 1939: 164.

The zoarium encrusts and surrounds the stems of the alcyonarian, *Leptogorgia virgulata*, forming fleshy cylindrical masses which have numerous short, lateral, round branches. An important diagnostic feature is that the zooecial aperture is not located on an oral prominence. There are 15 to 17 tentacles.

The color varies from grayish or white to transparent. Occasional specimens may be dark green in part, owing to the presence of unicellular green algae which sometimes coat them.

The zoarial lateral protuberances or branches range in size from 1.44 mm. to 9.0 mm. in length and have basal diameters of 1.0 mm. to 6.0 mm. The usual condition is about 5.28–7.68 mm. long and 3.84–5.28 mm. wide. Zooecia are 0.33–0.44 mm. long by 0.33–0.44 mm. wide.

Secondary growth in some specimens results in the formation of nodular sheaths which spread out over and around the primary zoarium, particularly in areas of the colony which are located at places of thick branching of the *Leptogorgia* stems. This condition is usually accompanied by a more gnarled appearance and longer (up to 15 mm.) erect portions.

The species is quite common in the Beaufort area and is found only on *Leptogorgia* stems. Marcus noted that the zoaria grow only around that portion of the alcyonarian axis devoid of polyps and cortex. This is also true of local colonies. Collections have been taken in Newport River, Beaufort harbor, Bogue Sound, and Cape Lookout.

Alcyonidium hauffi has previously been known only from the coast of Brazil, particularly at Perto de Santos.

Suborder PALUDICELLEA Allman, 1856 Family VICTORELLIDAE Hincks, 1880

Genus *Sundanella* Braem, 1939

Sundanella sibogae (Harmer), 1915. (Fig. 6.)

Victorella sibogae Harmer, 1915: 45.
Victorella sibogae, Marcus, 1937: 129.
Sundanella sibogae, Braem, 1939: 267.
Victorella sibogae, Osburn, 1940: 336.
Sundanella sibogae, Marcus, 1941: 69.
Sundanella sibogae, Osburn, 1947: 6.
Sundanella sibogae, Pearse and Williams, 1951: 137.

The zoarium is composed of elongate, erect, chitinous zooecia from which arise similar individuals by lateral budding. The primary individuals are adherent to the substrate but arise so close together that a thin stolon is only occasionally noticeable. Thus the primary individuals seem to be directly connected basally without an intervening stolon. Secondary individuals may develop at any distance from the base along the side, however, in most cases observed the secondary individuals arise from the lower half of the primary zooecia. The secondary zooecia may give rise to additional individuals and so on.

Each zooecium is quite tall, slender, cylindrical, squared at the tip, and slightly narrowed in some cases at the base. The maximum height observed was 3.08 mm., with 2.42 mm. being about average. The width measured 0.20–0.25 mm. The walls are thin, and yellowish when examined under a binocular microscope; however, when viewed with the unaided eye, they appear grayish-brown because of the presence of a thin coat of adherent earthy matter, reminiscent of *Nolella*. The number of tentacles is above 20.

The above description of Beaufort specimens, while agreeing generally with the descriptions of Braem, Marcus, and Osburn with respect to the form of the zoarium, tentacle number, and zooecial height, differs in several significant points. The zooecial width is one-half that reported by these workers. Also the zooecial wall is not circularly wrinkled in constriction, except for a slight indication in the basal portion of a few individuals. In the region of the orifice there

are no pectinate cuticular strips as described by Braem and Marcus. The mode of branching has a closer resemblance to that of *Victorella pavida* Kent than that figured for *S. sibogae* by Marcus (1941, fig. 38).

Beaufort specimens were collected from Newport River estuary in August, 1954. Colonies were growing over *Amathia convoluta* along with *Aeverrillia armata*, *Pedicellina cernua* and *Barentsia laxa*.

The species is now known to be distributed along the Atlantic coast from the Beaufort area south to Santos Bay, Brazil. Until the present record, its northern limit was the reefs off New River Inlet, North Carolina (Pearse and Williams).

Family NOLELLIDAE Harmer, 1915 Genus *Nolella* Gosse, 1855

Nolella stipata Gosse, 1855. (Fig. 7, 8.)

Nolella stipata Gosse, 1855: 35.
Farrella gigantea Busk, 1856: 93.
Farrella dilatata Hincks, 1860: 279.
Cylindroecium giganteum, Osburn, 1914: 218.
Nolella dilatata, Osburn, 1919: 607; 1923: 6D; 1940: 337.
Nolella gigantea, Marcus, 1937: 131.
Nolella dilatata, Marcus, 1938: 53.
Nolella gigantea, Osburn, 1940: 337; 1944: 17; 1947: 8.

The zooecia are elongate, cylindrical "posts", coated with earthy matter which imparts a grayish-brown or muddy color to them. They arise singly from a fine stolon. Until recently (Osburn, 1953: 737) the species was considered two, i.e., *Nolella gigantea* (Busk) which is tall with a narrow base at the stolon, and *N. dilatata* (Hincks) which is short with a basal dilation. Osburn considers them to be ecological variants, the form depending on the substrate over which they grow. Both forms are present at Beaufort. The *gigantea* form (Fig. 7) is by far the more common, ranging in height from 2.64 mm. to 3.00 mm. and 0.22 mm. in width. The *dilatata* form (Fig. 8) measures 0.72–1.00 mm. in height and 0.16–0.20 mm. in width.

Colonies adherent to soft substrates such as algae or hydroids, according to Osburn, have a much less prominent dilation than those adhering to a hard mollusk shell, where the dilation is very great. There is no such marked correlation in the case of Beaufort material. The *gigantea* form has been found on both soft and hard substrates but the *dilatata* form has been found only on hard substrates.

Nolella stipata has been collected in Newport River, Bogue Sound and in depths of forty feet at Beaufort Inlet and Cape Lookout.

The species is known on the Atlantic coast from Canada to Santos Bay, Brazil.

Genus *Anguinella* van Beneden, 1845

Anguinella palmata van Beneden, 1845. (Fig. 9.)

Anguinella palmata van Beneden, 1845: 34.
Anguinella palmata, Hincks, 1880a: 540.

Anguinella palmata, Osburn, 1912b: 253; 1914: 219; 1940: 338; 1944: 20.
Anguinella palmata, Marcus, 1937: 133.

The zoarium resembles a tuft of brown algae, being erect, irregularly branched in a somewhat palmate fashion, reaching up to 2.5 inches in height in the largest specimens. The zooecia are tubular, slightly curved inward, flat-tipped in younger branches to bluntly rounded in older ones, completely covered with earthy matter resulting in an opaque grayish-brown or dark brown color. The aperture is terminal; the tentacles number 10.

The zooecia measure about 0.12–0.15 mm. in diameter and vary in height up to 1.5 mm., depending on age. Zooecia which are attached to the substrate are much elongated and thickened, serving as a "stalk" for the colony. The axial zooecia of the branches as well as those of the stalk are devoid of functional polypides. New zooecia bud directly from older ones, so that each zooecium is capable of becoming the axis of a new branch.

The species grows abundantly on rock jetties in the sounds, as well as on shells and pilings. The zoarium is a common habitat for entoprocts and various stolonate ctenostomes.

Widely distributed on the Atlantic coasts of Europe and North America to Brazil, it has recently been reported by Osburn (1953) along the Pacific coast.

Suborder VESICULARINA Johnston, 1847
Family VESICULARIIDAE Johnston, 1838

Genus *Amathia* Lamouroux, 1812

Amathia convoluta Lamouroux, 1816. (Fig. 10, 11.)

Amathia convoluta Lamouroux, 1816: 160.
Amathia alternata, Verrill, 1878: 304.
Amathia alternata, Osburn, 1932b: 444.
Amathia convoluta, Marcus, 1937: 136.
Amathia convoluta, Osburn, 1940: 339; 1944: 23.

The zoarium is erect, jointed, and bushy; the horn-colored branches appear to be twisted in a tight spiral. The zooecia are erect, subcylindrical and closely connate to the tips, arranged in a double row which occupies most of an internode and which usually spirals counter-clockwise, making about one complete turn around the stem.

The zooecia at the proximal end of an internode measure 0.5–0.6 mm. in length, being slightly taller than the distal ones which are about 0.4 mm. The diameter is about 0.1–0.13 mm. at the base.

Locally, the species has been collected on shell substrates in the brackish estuaries, sounds and offshore. It is generally distributed along the east coast from Chesapeake Bay to Brazil.

A peculiar specimen of *Amathia* was collected at Fort Macon on Bogue Banks (August 24, 1954). The zoarium is 175 mm. high, which is much larger than most local *A. convoluta* colonies (75 mm. average), although the zooecial measurements

are within the same range. The zooecial rows rarely have even the slightest indication of a spiral, being characteristically arranged in a straight line along one side of the internode. The rows alternate sides from one internode to the next, though occasional rows may not be rotated quite 180° from that of the adjacent internode (Fig. 11). The stems are more uniform in diameter than in *A. convoluta*, and tend to be slightly smaller.

The specimen was determined by the writer to be the same as one deposited in the U. S. National Museum which was collected off Cape Fear, North Carolina (Sta. 2619, Albatross). The museum specimen was designated *Amathia spiralis* Lamouroux. However, neither specimen fits the description or figures of that species as it appears in Busk (1866: 34; Plate 6, fig. 2), Lamouroux's original description being unavailable.

Amathia vidovici Heller, 1867

Valkeria Vidovici Heller, 1867: 128–129.
Vesicularia dichotoma Verrill, 1874: 709.
Amathia dichotoma, Osburn, 1912b: 254.
Amathia vidovici, Osburn, 1940: 340; 1944: 21–22; 1947: 7.
Amathia vidovici, Hutchins, 1945: 538.
Amathia vidovici, Pearse and Williams, 1951: 137.

This species was not found during the present study but can be expected in future collections. It is distributed from Massachusetts southward to the Gulf of Mexico and the Caribbean Sea.

It is very similar in appearance to the following species except that the zooecia are only slightly connate and are grouped in four to eight pairs in a short spiral.

Amathia distans Busk, 1886. (Fig. 12.)

Amathia distans Busk, 1886: 33.
Amathia brasiliensis Busk, 1886: 34.
Amathia goodei Verrill, 1901b: 29.
? *Amathia goodei*, Osburn, 1914: 219.
Amathia distans, Marcus, 1937: 134.
Amathia distans, Osburn, 1940: 339; 1947: 7.
Amathia brasiliensis, Osburn, 1940: 339.

The zoarium is a delicate, dichotomously branching, white or brownish colony, which seldom exceeds 30–50 mm. in height. The internodes of the stems, which average 0.22 mm. in diameter, bear a partially spiraled double row of zooecia which may occupy the entire internode, or only the distal one-half or two-thirds of the internode, the latter condition being predominant.

The zooecia are about 0.40 mm. in height, closely connate to the tips in some specimens, or may be free at the tips and connate only at the base. Frequently the branches terminate in two long, barren internodes which sometimes give off one or two isolated zooecia or stunted branches at the nodes.

In the Challenger Reports, Busk described two species, *Amathia distans* and

A. brasiliensis, which differed in the diameter of the internodes, the degree of connation of the zooecia, the position of the zooecial rows on the stem, and barren terminal internodes. Marcus combined the two species under *A. distans* which has page priority, while Osburn maintained that the two species were distinct on the basis of Puerto Rico material. Beaufort specimens most commonly fall under Busk's description of *A. brasiliensis*, but do indicate intergradation with characters of his *A. distans*. On this basis the classification of Marcus is here accepted.

The species has been collected on dredged hydroids and *Amathia convoluta* colonies from Bogue Sound. It is sporadically abundant on Shark Shoal jetty and on oysters from Newport River.

It is distributed along the Atlantic coast from Beaufort to Brazil.

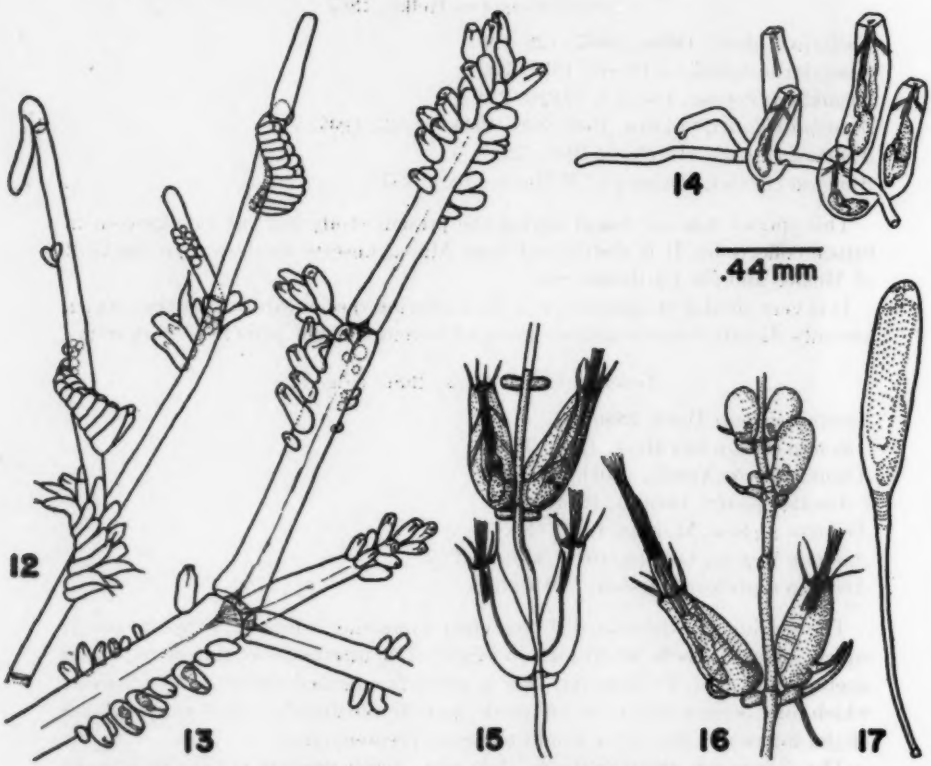


FIG. 12. *Amathia distans* Busk. FIG. 13. *Zoobotryon verticillatum* (delle Chiaje). FIG. 14. *Bowerbankia gracilis* Leidy. FIG. 15. *Aeverrillia armata* (Verrill), showing partly extended setigerous collars. FIG. 16. *Aeverrillia setigera* (Hincks), showing caudate processes and setigerous collars. Note secondary and tertiary stolons arising at lower right. FIG. 17. *Triticella elongata* (Osburn), commensal on crabs; stolon not shown. (Fig. 12, 13 are same scale as Fig. 10; others are to scale of Fig. 14.)

Genus *Zoobotryon* Ehrenberg, 1831

Zoobotryon verticillatum (delle Chiaje), 1828. (Fig. 13.)

Hydra verticillata delle Chiaje, 1828: 203.
Zoobotryon pellucidus Ehrenberg, 1831; no pagination.
Zoobotryon pellucidum, Marcus, 1937: 139.
Zoobotryon pellucidum, Osburn, 1940: 341.

The zooarium is a large, transparent, dichotomous or trichotomous branching colony in which the zooecia are arranged in two rows, one on each side of the older internodes, or clustered irregularly at the distal end of the younger internodes and growing points. The colony is quite flaccid, though able to spread out in water.

The diameter of the internode varies in Beaufort specimens from 0.22 mm. to 1.0 mm. The zooecia are somewhat elongate, narrowed at the base, and of irregular sizes.

The colonies have been dredged from Bogue Sound and found in great masses in tide pools along the outer banks. None of the specimens have been collected attached, which suggests that the species drifts in from offshore and warmer waters to the south. The species is circumtropical (Osburn, 1940), distributed on the east coast from Bermuda and Florida throughout the Caribbean and Gulf of Mexico to Brazil.

Genus *Bowerbankia* Farre, 1837

Bowerbankia gracilis Leidy, 1855. (Fig. 14.)

Bowerbankia gracilis Leidy, 1855: 142.
Vesicularia gracilis, Verrill and Smith, 1874: 709.
Valkeria caudata Hincks, 1877: 215.
Vesicularia gracilis, Verrill, 1879c: 28.
Bowerbankia caudata, Hincks, 1880a: 521.
Bowerbankia gracilis, Osburn, 1912a: 287; 1912b: 253; 1914: 218; 1927: 123; 1932a: 366; 1933: 63; 1940: 341; 1944: 23; 1947: 7.
Bowerbankia caudata, Osburn, 1919: 607.
Bowerbankia gracilis, Marcus, 1938: 56.
Bowerbankia gracilis, Rogick and Croasdale, 1949: 47.

The zoarium is stolonate, creeping over stems of hydroids, algae and other ctenostomes. The zooecia arise singly, in pairs, or clustered along the slender, transparent stolon which may be free from the substrate for short distances.

Zooecia are transparent, showing clearly the details of the polypides, elongate, squared at the tips and narrowed at the base. They measure about 0.70 mm. in height and 0.15 mm. in width. Occasional zooecia may have a short caudate process near the base; this condition was the basis for establishing *Bowerbankia caudata* Hincks which Osburn considers synonomous with *B. gracilis*. The stolon is 0.05 mm. in diameter and divided at intervals into internodes by diaphragms each perforated by a pore.

The dimensions of Beaufort specimens are slightly smaller than those listed by Osburn for Chesapeake Bay and Pacific coast material. This may be because of the small number of collections found and examined during the present study.

The species appears to be a shallow water form distributed from Greenland to Brazil and also along the Pacific coast of North America.

Suborder STOLONIFERA Ehlers, 1876 Family VALKERIIDAE Hincks, 1877

Genus *Aeverrillia* Marcus, 1941

Aeverrillia armata (Verrill), 1874. (Fig. 15.)

Vesicularia armata Verrill, 1874: 710.
Vesicularia armata, Verrill, 1878: 304; 1879c: 28.
Hippuraria armata, Osburn, 1912b: 256.
Buskia armata, Osburn, 1933: 63.
Buverrillia armata, Marcus, 1941: 76.
Aeverrillia armata, Osburn, 1944: 25.
Aeskia armata, Hutchins, 1945: 538.
Aeverrillia armata, Rogick and Croasdale, 1949: 45.

The zooarium consists of a very slender, segmented stolon from which the zooecia arise in pairs, one on each side, on minute lateral segments at the distal end of the internodes. The absence of basal clasping processes on the zooecia immediately distinguishes this species from *Aeverrillia setigera*.

The stolon is well chitinized, tough, and rather loosely creeping and entwined on the substrate. It measures 0.03 mm. in diameter. The zooecia are elongate-ovoid, 0.55–0.60 mm. tall and 0.175 mm. in diameter at the widest part which is near the base. The side of the zooecium facing the stolon is slightly less chitinized than the rest and is distinctly flattened. In each of the four corners of the distal (oral) end of the zooecium a spine arises on a short prominence. These spines, which are 0.12–0.20 mm. in length, are pointed upward when the tentacles are retracted and somewhat laterally during tentacle protrusion. In most preserved specimens the oral setae or setigerous collar is fully extended though generally not unfurled. This collar is quite obvious, measuring 0.45–0.50 mm. in length. Occasionally the eight tentacles may be observed within the unfurled collar. The polypide is supplied with a distinct gizzard consisting of four conical lobes with chitinized teeth.

The species is reported from Maine to Brazil though it has not been found in the tropical waters. It has been collected locally on the stems of *Pennaria tiarella* and *Amathia convoluta* from regions of lowered salinity as Newport River, in Bogue Sound and from oceanic conditions to forty feet of water off Fort Macon, west of Beaufort Inlet. Sutcliffe (1947) found it on algae from the jetty at Cape Lookout. Osburn has reported it from waters of the Chesapeake Bay with a salinity as low as 12‰.

Aeverrillia setigera (Hincks), 1887. (Fig. 16.)

Buskia setigera Hincks, 1887: 127.
Buskia setigera, Marcus, 1937: 142.

Aeverrillia setigera, Marcus, 1941: 74.
Buskia setigera, Hutchins, 1945: 539.
Aeverrillia setigera, Rogick, 1954b: 201.
Aeverrillia setigera, Rogick and Croasdale, 1949: 45.

This species is quite similar to the preceding one, differing in that the zooecia have one or more caudate clasping processes located basally, and the stolons may be much branched, giving rise to secondary and tertiary stolons, the designation depending on the points of origin.

The flattened area of most of the zooecia is not as conspicuous as in *Aeverrillia armata*. The zooecia arise in pairs; however, an occasional mate may be missing although the basal segment or secondary stolon is present. They tend to be recumbent with the clasping processes wrapped tightly around the substrate which is usually a hydroid stem such as *Pennaria*. The clasping processes may also adhere to the primary stolon or to the side branches and appear to anastomose with them in some instances. The distal end of the zooecium bears four long hollow spines which arise from strong prominences but are separated from the latter by septa. The zooecia are about 0.55 mm. in length and 0.175 mm. in width at the widest part. The distal spines measure 0.15 mm. and the clasping processes are about 0.18 mm. long.

The primary stolon measures about 0.04 mm. in diameter; each of its internodes is slightly enlarged at the distal end where it is separated from the next internode and the two lateral secondary internodes by septa each perforated by a single pore. The tertiary stolons have the smallest diameters and arise at various angles from the secondary stolons, being separated by a perforated septum from the latter.

Aeverrillia setigera is very difficult to remove from the substrate because of the firmly adherent clasping processes, whereas *A. armata* generally can be pulled loose intact.

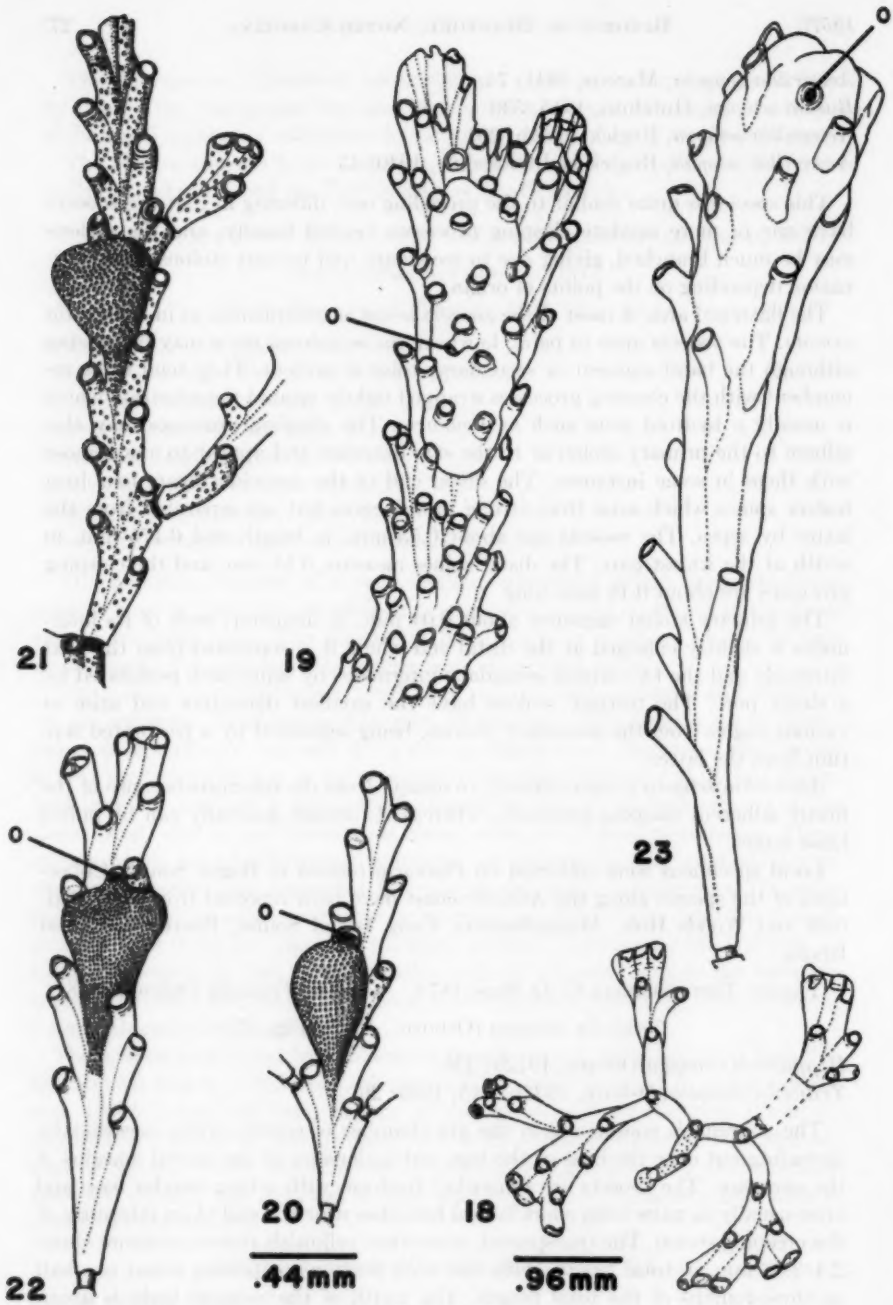
Local specimens were collected on *Pennaria tiarella* in Bogue Sound. Collections of the species along the Atlantic coast have been reported from New Bedford and Woods Hole, Massachusetts, Long Island Sound, Puerto Rico, and Brazil.

Family TRITICELLIDAE G. O. Sars, 1874 Genus *Triticella* Dalyell, 1848

Triticella elongata (Osburn), 1912. (Fig. 17.)

Hippuraria elongata Osburn, 1912b: 256.
Triticella elongata, Osburn, 1932b: 445; 1944: 26.

The zoarium is commensal in the gill chamber of certain crabs, occasionally spreading out over the base of the legs and undersides of the lateral margins of the carapace. The zooecia are somewhat fusiform with a long slender base and arise usually in pairs from short lateral branches near the end of an internode of the creeping stolon. The transparent, somewhat yellowish zooecia measure about 2.4–3.08 mm. in total length, with the stalk portion comprising about one-half to three-fourths of the total length. The width of the zooecial body is about 0.22 mm.



FIGS. 18–23

The species was collected locally on *Callinectes sapidus* and on the commensal crab *Pinnixia chaetopterana* found in *Chaetopterus variopedatus* tubes. DeTurk (1940) found the species commensal on the crabs *Callinectes sapidus*, *Libinia emarginata*, *Libinia dubia*, and *Hepatus epheliticus*.

Colonies collected on July 13, 1955, were reproducing.

The species is distributed from Vineyard Sound, Massachusetts, to Beaufort.

Order CYLCOSTOMATA Busk, 1852 Suborder TUBULIPORINA Hagenow, 1851

Family ONCOUSOECIIDAE Canu, 1918 Genus *Proboscina* Audouin, 1826

Proboscina species. (Fig. 18.)

The single specimen collected was on a skate egg case washed ashore at Fort Macon. No ovicells were present, hence positive determination could not be made. It is provisionally assigned here to the genus *Proboscina* as defined by Osburn (1953: 618–620) and strikingly resembles his figure of *P. incrassata* (Smitt) (Plate 66, fig. 1).

The zoarium is adnate, uniserial for only a short distance at the proximal end, then becoming biserial or with additional zooecia over most of the length of the linear lobes. Peristomes are somewhat erect, projecting 0.20–0.25 mm. high; the terminal orifices are 0.11–0.13 mm. in diameter.

An examination of the condition of other Bryozoa, hydroids, and barnacles encrusting the egg case showed little evidence of wear; even delicate colonies of *Aetea anguina* were intact. This suggests that the species occurs offshore in the near vicinity. If the colony is not from the Beaufort area, it probably drifted from waters to the south because of the prevailing currents.

Family DIASTOPORIDAE Gregory, 1899 Genus *Diaperoecia* Canu, 1918

Diaperoecia floridana Osburn, 1940. (Fig. 19.)

Idmonea milneana Smitt, 1872: 8 (*non* D'Orbigny, 1839).
Diaperoecia radicata Canu and Bassler, 1928: 160 (*non* Kirkpatrick, 1888).
Diaperoecia floridana Osburn, 1940: 331; 1947: 5.
? *Diaperoecia rugosa* Osburn, 1940: 332.

The zoarium is erect, irregularly branched, without joints, transversely wrinkled dorsally and ventrally. Branches are composed of tubular zooecia which are free distally and tend to be arranged in transverse rows. The ovicell or ooecium encloses several zooecia and has a centrally located ooeciostome which is recurved toward the base.

FIG. 18. *Proboscina* sp., young zoarium. FIG. 19. *Diaperoecia floridana* Osburn, portion of branch showing ooecium with central ooeciostome (o); detail as in Fig. 21. FIG. 20 *Crisia eburnea* (Linnaeus), fertile internode showing detail of ooecium, ooeciostome (o), and one zooecium. FIG. 21. *Crisia elongata* Milne Edwards, ooeciostome missing. FIG. 22. *Crisia ramosa* Harmer, ooeciostome (o) damaged and not showing characteristic shape; detail of ooecium. FIG. 23. *Crisulipora orientalis* Canu and Bassler, showing fertile internode and subterminal ooeciostome (o); detail as in Fig. 21. (Fig. 18, 19 are same scale; Fig. 20–23 are same scale.)

Osburn's original description states: "There is considerable variation in the width of the branches, ordinarily from 0.70 to 1.00 mm., often a little wider near a bifurcation and occasionally narrower branches occur. Five or six tubules, seven or eight near a bifurcation, make up the width of a branch; the free portions of the tubules have some tendency to occur in diagonal rows, and the lateral ones may be connate for a part of their length . . . free portions of the tubules are about 0.40 mm. long, somewhat wrinkled, slightly tapering, the orifice usually quite round."

The ooecium is irregularly elongate, about 2.50 mm. long and 0.90 mm. wide. The ooeciostome and ooeciopore are elliptical, the former about the width of a zooecium (0.16–0.20 mm.). Occasionally the ooecium may spread over the base of a bifurcation, in which case the ooeciostome is located near the fork rather than in a central position.

The species was originally described from specimens taken from the "fishing bank" off Beaufort at thirteen fathoms. Specimens of the species were not collected during the present study but Dr. Osburn has kindly loaned the writer material from the type locality for study.

In the Atlantic the species is reported from Beaufort, Florida, Puerto Rico and the Gulf of Mexico.

Suborder ARTICULATA Busk, 1859 Family CRISIIDAE Johnston, 1838

Genus *Crisia* Lamouroux, 1812

Crisia eburnea (Linnaeus), 1758. (Fig. 20.)

Sertularia eburnea Linnaeus, 1758: 810.
Crisia eburnea, Verrill, 1878: 304.
Crisia eburnea, Osburn, 1912a: 276; 1912b: 215; 1919: 606; 1923: 5D; 1933: 8; 1944: 12.
Crisia eburnea, Hutchins, 1945: 536.
Crisia eburnea, Rogick and Croasdale, 1949: 54.
Crisia eburnea, Pearse and Williams, 1951: 137.

The zoarium is erect and jointed, with branches curving slightly inward. The ovicell is elongate, greatly inflated distally and has a short ooeciostome bending forward; the ooeciopore is elliptical and transverse. Internodes generally have 5 to 7 tubular, connate zooecia arranged alternately, though they may have more (4 to 11 in a sterile internode, 7 to 10 in a fertile one). The ovicell usually replaces the second or third zooecium in the fertile internodes. The chitinous joints vary in color from yellowish to brown, being darkest in older portions of the colony.

The colonies form white, bushy tufts on rocks and the stems of larger algae. In the Beaufort region the species is not found in the brackish estuaries and sounds, but penetrates only as far as the Fort Macon jetties. It is quite common on *Zonaria* and *Sargassum* from dredging or drift collections along the ocean side of the outer banks.

The species is well known along the Atlantic coast of North America from Greenland and Labrador south to North Carolina.

Crisia elongata Milne Edwards, 1838. (Fig. 21.)

Crisia elongata Milne Edwards, 1838: 203.
Crisia eburnea form *denticulata* Smitt, 1872: 4.
? *Crisia denticulata*, Osburn, 1914: 185.
Crisia denticulata, Canu and Bassler, 1928: 156.
Crisia elongata, Canu and Bassler, 1928: 157.
Crisia elongata, Osburn, 1940: 328; 1947: 3.
Crisia elongata, Pearse and Williams, 1951: 137.

The zoarium is jointed and has slender, elongate branches; there are about 14 or 16 zooecia to an internode though ranges have been reported from 6 to 30. The tubular zooecia are arranged alternately and fused so as to make the inner (medial) outlines almost indistinguishable; the peristomes are short and sharply turned forward. The frontal (ventral) surface on the internode sometimes appears to have a faint median keel or ridge formed by the convergence of the zooecia. The ovicell is short, broad, and sharply inflated, with a very short ooeciostome or none at all; the ooeciopore is a transverse slit. Joints between the internodes are jet black, although in younger portions of the colony they may be brown or even yellowish.

The species was not collected during the present study, but Pearse and Williams have reported it from the reefs off New River Inlet, North Carolina, in 40 to 55 feet. It can probably be expected at similar depths offshore from Beaufort.

Crisia ramosa Harmer, 1891. (Fig. 22.)

Crisia ramosa Harmer, 1891: 134.
Crisia ramosa, Marcus, 1937: 17.
Crisia ramosa, Osburn, 1940: 329.

The zoarium is erect, typically with colorless, chitinous joints separating the internodes. The ooecium is large, pyriform, gently inflated distally, and usually occupies an intermediate position between the fifth and seventh pairs of zooecia. The terminal ooeciostome is flared or trumpet-shaped with a round ooeciopore. Zooecia always have a free tubular portion which is bent strongly toward the frontal plane of the branch. The number of zooecia constituting an internode is variable, up to 22 in the infertile internodes and 29 in fertile ones (Calvert, 1931).

Specimens loaned by Dr. Osburn from the "fishing banks" have brown joints instead of the colorless ones as reported in most descriptions of the species. Perhaps this is due to the fact that the specimens were dry-mounted. Unfortunately, the ooeciostomes in the preparations are damaged, hence the figure does not show the characteristic shape.

The species is reported on the Atlantic coast from Beaufort, Puerto Rico, and Brazil.

Genus *Crisulipora* Robertson, 1910

Crisulipora orientalis Canu and Bassler, 1928. (Fig. 23.)

Crisulipora orientalis Canu and Bassler, 1928: 162.
Crisulipora orientalis, Osburn, 1940: 332; 1947: 4.
Crisulipora orientalis, Pearse and Williams, 1951: 137.

"The zoarium is attached to floating bodies; it is articulated and formed of claviform bi- to trifurcate segments in which the non-cellular face is plain or concave. The tubes are distinct, separated by a furrow, finely striated transversely by lines of punctations, terminated by a long, free, arched and erect peristome. The peristome is thin and orbicular" (Canu and Bassler, 1928).

Beaufort specimens do not show the branching of the internodes but agree in all other respects. The ovicell is very long, extending most of the length of the internode, and is traversed by the zooecia. It is narrowest proximally, widest distally, and rather gently inflated. The ooeciostome is subterminal and only slightly developed; the ooeciopore is circular. The ovicell greatly accentuates the club-shaped appearance of the internodes.

The lateral zooecia of the fertile internodes may face dorsally, thus enhancing the characteristic concavity of the dorsal surface.

The species is reported locally by Osburn from the "fishing banks" (13 fathoms). Pearse and Williams found it in shallow water from 15 to 20 feet on the reefs off New River Inlet. It is distributed from the Florida keys and Puerto Rico, north to Beaufort.

Order CHEILOSTOMATA Busk, 1852 Suborder ANASCA Levinsen, 1909

Division I INOVICELLATA Jullien, 1888

Family AETEIDAE Smitt, 1867 Genus *Aetea* Lamouroux, 1812

Aetea anguina (Linnaeus), 1758. (Fig. 24.)

Sertularia anguina Linnaeus, 1758: 816.
Aetea anguina Verrill and Smith, 1874: 710.
Aetea anguina, Verrill, 1878: 304; 1879c: 28.
Aetea anguina, Osburn, 1912b: 220; 1933: 18; 1940: 345; 1944: 28; 1947: 8.
Aetea anguina, Marcus, 1937: 26.
Aetea anguina, Hutchins, 1945: 539.
Aetea anguina, Pearse and Williams, 1951: 137.

The zoarium is calcareous, white, and has an adnate stolon consisting of club-shaped expansions which give rise to the erect, usually recurved, tubular portions of the zooecia. The erect tubes are slightly enlarged and spoon-shaped distally, with a flat membranous area on one side and a terminal operculum. Very fine annulations appear on the tubes from the base to the proximal end of the membranous area, whereas the remainder of the distal portion is finely punctate.

Rogick (Rogick and Croasdale, 1949: 43), following Marcus's criteria for distinguishing this species from *Aetea sica* (Couch), states that the ratio of aperture

(membranous area) length to width is between 1.7:1 and 2:1 for *A. anguina* and between 2.6:1 and 4:1 for *A. sica*. On this basis some of the Beaufort material should be designated *A. sica*. However, Osburn (1940) separates the two species by characterizing *A. sica* as having the erect portion straighter, the "head" longer and narrower, the operculum set more transversely across the end of the zooecial tube, and the punctations of the swollen basal tube so distributed as to give the effect of annulation. The latter feature is not evident in any local material, nor do Rogick's figures of *A. sica* (*loc. cit.*, p. 42, figs. 1–3) show this characteristic. For these reasons it is difficult to decide whether we are concerned here with one, or two, species. However, Osburn's diagnosis is herein accepted and the species is taken to be *A. anguina*.

Aetea anguina is quite common in all collections of shells and algae from offshore. It is particularly abundant on *Zonaria* and *Sargassum*. The species appears to reach its maximum inshore development on logs and rocks of the outer jetty at Fort Macon, though colonies have settled on experimental tiles during the summer as far as a mile up Newport River estuary.

It is widely distributed, occurring on the Atlantic coast from Maine to Brazil.

Division II MALACOSTEGA Levinsen, 1909

Family MEMBRANIPORIDAE Busk, 1854

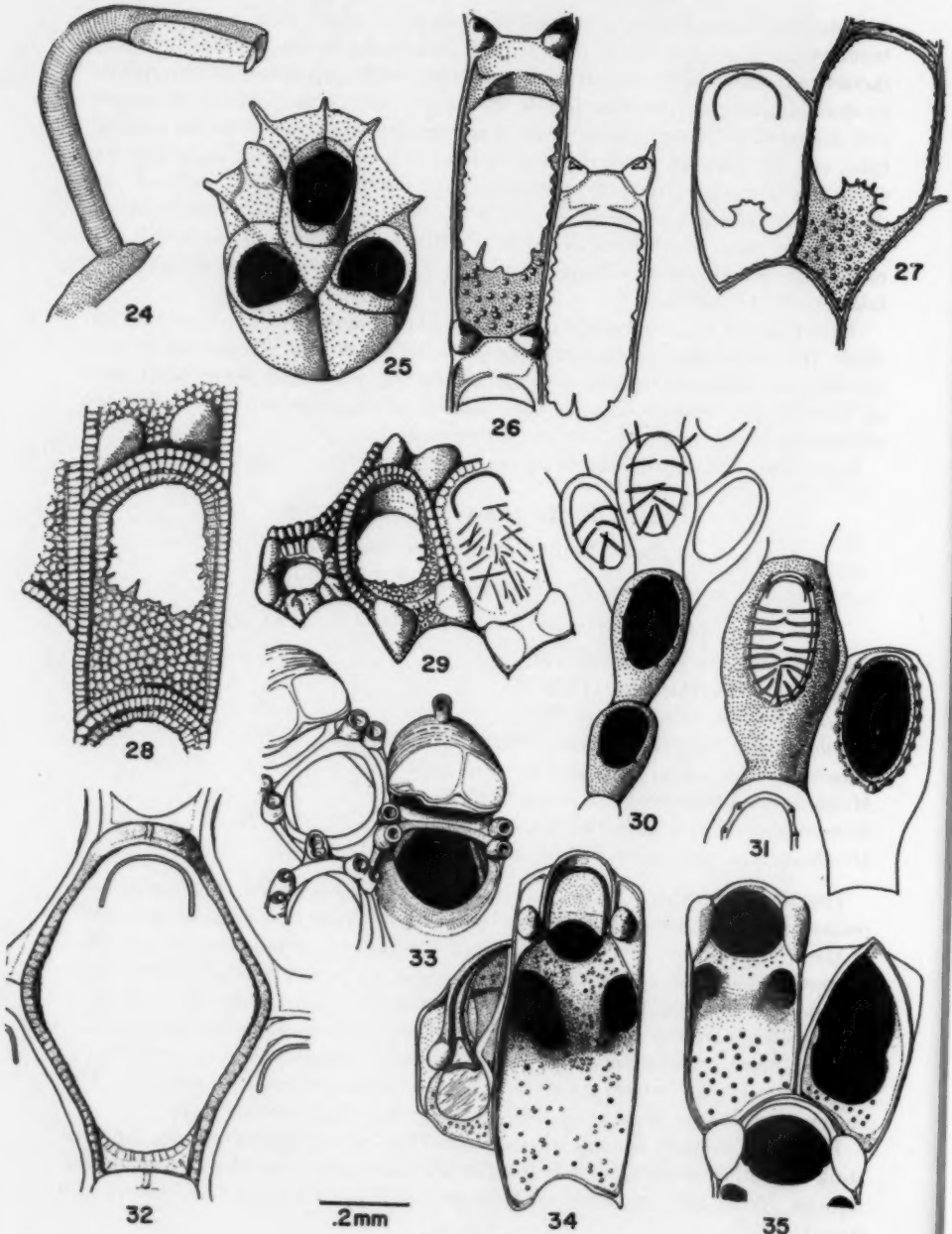
Genus *Membranipora* Blainville, 1830

Membranipora tuberculata (Bosc), 1802. (Fig. 25, 26.)

Flustra tuberculata Bosc, 1802: 143.
Flustra tehuelcha d'Orbigny, 1839: 17.
Biflustra dentata, Verrill, 1900: 594.
Membranipora tehuelcha, Osburn, 1912b: 231; 1914: 193.
Nitscheina tuberculata, Canu and Bassler, 1928: 18.
Membranipora tuberculata, Marcus, 1937: 33.
Membranipora tuberculata, Osburn, 1940: 349; 1944: 30; 1947: 9.
Membranipora tuberculata, Rogick and Croasdale, 1949: 63.

The zoarium forms a white, lacy crust on drifting seaweed. The zooecia are rectangular with a large membranous frontal area. Under the proximal one-fourth of the frontal surface is a calcareous shelf (cryptocyst) which may be extended narrowly along the edges of the thin lateral walls and produced into short spinules which project medially. The cryptocyst slants slightly dorsally as it progresses toward the center of the zooecium and from its surface arise numerous minute, blunt protuberances. At the distal end of the zooecium are two heavy, rounded tubercles which give the colonies a characteristic appearance. Occasionally these tubercles may coalesce along the distal zooecial wall.

Projecting dorsally toward the substrate from the cryptocyst are one to three stalk-like processes which bear spicules arranged in a comb-like fashion. Other minute, irregularly branched spicules protrude inward from the base of the zooecial walls.



FIGS. 24–35

The ancestrula, the primary individual of the colony, is twinned, inflated, and has the membranous area greatly reduced (Fig. 25).

This species is the commonest bryozoan found on floating *Sargassum* and is occasionally on *Zonaria*. It is found along the Atlantic coast wherever *Sargassum* is distributed by ocean currents but it is properly considered a circumtropical species.

Membranipora savartii (Audouin), 1826. (Fig. 27.)

Flustra savartii Audouin, 1826: 240.
Biflustra savartii, Smitt, 1873: 20.
Membranipora savartii, Osburn, 1914: 194.
Acanthodesia savarti, Canu and Bassler, 1923: 31; 1928: 14.
Acanthodesia savartii, Marcus, 1937: 40.
Acanthodesia savartii, Osburn, 1940: 352.
Acanthodesia savarti, Osburn, 1947: 9.

The zoarium is encrusting; the zooecia are immediately recognizable by the presence of a well-developed proximal cryptocyst which possesses a characteristic broad, denticulate process projecting into the large orifice beneath the frontal membrane (opesia).

The zooecia are elongate, quadrangular, and outlined by a thin mural rim which is irregularly studded by minute tubercles. The cryptocyst also bears tiny tubercules and its thin lateral and distal extensions around the opesia are distinguishable only by these processes.

Whether or not the species is to be considered an accidental one in the Beaufort area remains to be seen. It is normally distributed in warmer waters from Florida to Brazil. The specimens were collected on a bottle from the beach drift on Bogue Bank (October 9, 1954, about a month after Hurricanes "Carol" and "Edna"). It is conceivable that the tropical storms were responsible for its being washed ashore here from waters farther south.

Membranipora tenuis Desor, 1848. (Fig. 28.)

Membranipora tenuis Desor, 1848: 66.
Biflustra denticulata Smitt, 1873: 18.

FIG. 24. *Aetea anguina* (Linnaeus), with operculum open. FIG. 25. *Membranipora tuberculata* (Bosc), twinned ancestrula and one new zooecium. FIG. 26. The same, showing detail of mature zooecium. FIG. 27. *Membranipora savartii* (Audouin). Right, detail of zooecium with frontal membrane removed; left, intact zooecium. FIG. 28. *Membranipora tenuis* Desor, detail of zooecium. FIG. 29. *Conopeum commensale* Kirkpatrick and Metzelaar. Left, abortive zooecium; middle, detail of zooecium with ectocyst removed; right, ectocyst intact, showing chitinous spinules and heavy outline around tubercles. FIG. 30. *Electra crustulenta* (Pallas), portion of zoarium showing ancestrula (bottom) and one zooecium in detail. FIG. 31. *Electra hastingsae* Marcus. Note median proximal spine. FIG. 32. *Aplousina gigantea* Canu and Bassler, with endozooecial ovicell. FIG. 33. *Chaperia galeata* (Busk), with ovicells and avicularia; spines missing except for bases. FIG. 34. *Thalamoporella falcifera* Hincks, with operculum and avicularium mandible intact. FIG. 35. *Thalamoporella gothica* var. *floridana* Osburn, showing interzooecial avicularium with appearance of a gothic arch. (All the same scale.)

Membranipora tenuis, Verrill and Smith, 1874: 712.
Biflustra denticulata, Verrill, 1878: 305.
Membranipora tenuis, Osburn, 1912b: 231.
Hemiseptella grandicella, Canu and Bassler, 1923: 71.
Hemiseptella tuberosa Canu and Bassler, 1923: 71.
Hemiseptella denticulata, Canu and Bassler, 1928: 62.
Hemiseptella hexagonalis Canu and Bassler, 1928: 63.
Acanthodesia tenuis, Marcus, 1937: 42.
Acanthodesia tenuis, Osburn, 1940: 353; 1944: 35; 1947: 9.
Acanthodesia tenuis, Hutchins, 1945: 539.
Membranipora tenuis, Pearse and Williams, 1951: 137.

The zoarium is encrusting, unilaminate or multilaminate, composed of elongate, rectangular or quadrangular zooecia with membranous frontal surfaces. The zooecia surrounding the twinned ancestrula are usually hexagonal as may be other zooecia in crowded conditions. The cryptocyst forms a broad shelf under the frontal area and is typically well developed, occupying the proximal half of the zooecium, thence extending narrowly around the zooecial walls to the distal end. Its surface is granulated and from its irregular border short spines or spicules project inward. The extent of the cryptocyst development is quite variable, often being reduced to only a narrow, irregularly serrated border. Osburn (1940) illustrates many of the variations from Beaufort material.

The mural rim is finely beaded and separated from adjacent zooecial walls by a distinct line. One or two low, blunt tubercles are sometimes present at the proximal corners of the zooecia.

The polypide has about ten tentacles.

This common species is widely distributed in the Beaufort area on almost any substrate, and has a wide range of salinity tolerance. Magalhaes (1948) reports the species as a very common consortes on various species of *Busycon*. The writer has found it especially abundant on another gastropod, *Cantharus tinctus*. It occurs on the Atlantic coast from Massachusetts to Brazil.

Genus *Conopeum* Gray, 1848

Conopeum commensale Kirkpatrick and Metzelaar, 1922. (Fig. 29.)

Conopeum commensale Kirkpatrick and Metzelaar, 1922: 985.
Conopeum commensale, Marcus, 1937: 35; 1938: 16; 1939: 126.
Conopeum commensale, Pearse and Williams, 1951: 137.

The zoarium forms uni- or multilaminate crusts on shells and alcyonarian stems. The zooecia are variable in shape, elongate quadrangular or hexagonal or frequently rounded at the distal ends, the outlines distinctly marked by a dark brown line. The frontal surface is membranous and thickly covered with slender chitinous spinules. The proximal corners of the zooecia bear two rounded tubercles, though occasionally only one or none is present. A granulated cryptocyst descends rapidly and is extended narrowly around the lateral and distal walls to

enclose an ovoid opesia. The opercular margin is heavily chitinized and brownish in color.

Much variation appears in the distribution and size of the chitinous spinules on the frontal membrane (ectocyst). In some specimens they are limited to the margins of the ectocyst, while in others they may spread densely or sparsely over the whole surface. Rarely, portions of colonies show no indication of spinules. The more marginal spinules are most frequently the longest and usually pointed inward, though all spinules may be of equal size and erect.

The brown outlines delineate the beaded or granulated mural rims as well as the tubercles. If the tubercles are separate, each is outlined; whereas, if they have fused, they are marked as a single quadrangular block.

Conopeum commensale may be easily mistaken for forms of *Membranipora tenuis* having proximal tubercles and poorly developed cryptocysts. However, if the ectocyst or frontal membrane is present, the chitinous spinules will immediately prevent confusion. The brown line around the tubercles in *C. commensale* is also a helpful character.

The multilaminate tendency of the colonies was well illustrated by zoaria of at least ten layers found on a shell dredged from Bogue Sound. Specimens were also multilaminate on the stems of *Leptogorgia virgulata*.

Its occurrence at Beaufort appears to be the northernmost record on the Atlantic coast, the species being distributed in warmer waters south to Brazil. Pearse and Williams record it at the New River Inlet reefs at forty feet. It was found at Beaufort in Bogue Sound and at forty feet in depth off Cape Lookout.

Family ELECTRINIDAE d'Orbigny, 1851 Genus *Electra* Lamouroux, 1816

Electra crustulenta (Pallas), 1766. (Fig. 30.)

Eschara crustulenta Pallas, 1766: 39
Membranipora lacroixii, Osburn, 1912b: 227 (in part).
Electra crustulenta, Borg, 1931: 29 (discussion).
Membranipora crustulenta, Osburn, 1944: 31.

The zoarium is a very delicate layer of ramifying series of zooecia. The zooecia are small, somewhat pyriform, with an oval aperture which is arched over by a series of spines. The zooecia are about 0.30 mm. long and 0.18 mm. wide, narrowed proximally, and have a moderately developed gymnocyst which extends about one-fourth of the zooecial length. The number of spines around the frontal area is variable; however, there is usually a semi-erect spine on either side at the distal end of the rim and about two to four spines distributed on each side which project over the area. There is never a median proximal spine as in *E. hastingsae*. *Electra crustulenta* is reported to have a calcareous operculum, but none of the Beaufort specimens exhibited this feature.

The species has a characteristic growth pattern as pointed out by Osburn (1944) in which the ancestrula buds off a zooecium proximally and distally, each of which gives rise to three more.

Beaufort specimens are much smaller than those reported by Osburn and

others. The spines are longer than those shown in figures by Osburn from Chesapeake Bay material and the gymnocyst is better developed.

The species is periodically abundant on shells and the experimental tiles located in the estuarine conditions of Newport River. Because of the confusion of the taxonomy of this species, its range is vague. Its probable range on the Atlantic coast is from Woods Hole to Beaufort.

Electra hastingsae Marcus, 1938. (Fig. 31.)

Escharina lineata Leidy, 1855: 141.
Membranipora lineata, Verrill and Smith, 1874: 712.
Membranipora lineata, Verrill, 1878: 304.
Membranipora monostachys, Osburn, 1912b: 227 (in part).
Electra monostachys, Osburn, 1933: 20.
Electra hastingsae Marcus, 1938: 17 (new name).
Electra hastingsae, Osburn, 1944: 39.
Electra hastingsae, Hutchins, 1945: 540.
Electra hastingsae, Rogick and Croasdale, 1949: 55.

The zoarium forms a crust which delicately branches in one or more series over the substrate. The zooecia are smooth-surfaced, elongate and somewhat pyriform, the proximal portion or gymnocyst being noticeably narrowed and shallow. The gymnocyst extends about one-fourth to one-half of the zooecial length. The oval membranous area (opesium) is surrounded by a raised mural rim from which arise numerous spines which arch over the opesium. Though the number of spines is variable, the usual number and arrangement is as follows: an erect or semi-erect disto-lateral spine on either side at the level of the operculum, about eight curved spines along each side, and a strong median proximal spine which has a somewhat thickened base. In specimens in which the spines have been lost or removed, the location of the spines is marked by small hollow knobs.

Electra hastingsae is commonly found on shells and rocks in the sounds and offshore but rarely occurs on flexible substrates such as algae. A shell substrate from which the zoarium has been removed is usually characteristically etched in the form of a series of elongate ovoid pits which mark the site of each zooecium.

This species may easily be confused with *E. crustulenta* (Pallas) which is also present in the area; however, the latter lacks the median proximal spine and is smaller in size.

E. hastingsae is distributed from Maine to Brazil.

Family HINCKSINIDAE Canu and Bassler, 1927
Genus *Aplousina* Canu and Bassler, 1927

Aplousina gigantea Canu and Bassler, 1927. (Fig. 32.)

Aplousina gigantea Canu and Bassler, 1927: 3; 1928: 20.
? *Aplousina gigantea*, Osburn, 1940: 357.

The zoarium is encrusting, lace-like in appearance, and composed of very large, ovoid zooecia with narrow mural rims. The entire frontal area of the

zooecia is membranous, with an occasional poorly developed, smooth, proximal cryptocyst evident. The zooecia are 0.77–1.10 mm. in length and 0.44–0.66 mm. in width; the operculum is 0.20 mm. wide at the base and is heavily chitinized around its margin. The mural rim is granulated or slightly beaded. The ovicell is endozooecial, i.e., formed by the forward extension of the distal zooecial wall, very small, transverse, only slightly elevated, and frequently has a frontal callosity (median roughened area).

The species is rare in the Beaufort area. The several specimens studied were collected from depths of three fathoms in Bogue Sound by Dr. Osburn.

It has previously been reported from the Straits of Florida and the Gulf of Mexico in 30 to 56 fathoms. Osburn's questioned record from Puerto Rico was of five fathoms.

Family CHAPERIIDAE Jullien, 1888 Genus *Chaperia* Jullien, 1881

Chaperia galeata (Busk), 1852. (Fig. 33.)

Membranipora galeata Busk, 1854: 62.

The zoarium is pink- or orange-tinted in living specimens, encrusting algae. Zooecia are of moderate size, about 0.40 mm. long and 0.22–0.35 mm. wide; ovate to elliptical. The opesium occupies most of the frontal area and generally is widest distally with a nearly straight distal margin. A narrow, smooth, flat shelf (cryptocyst?) extends around the proximal and lateral borders of the opesium. The rather narrow mural rim arises disto-laterally, reaching its highest elevation and greatest thickness around the distal margin on the zooecium. Projecting from hollow tubercles at the disto-lateral corners of the mural rim are two pairs of long hollow spines which are attached by means of brownish chitinous joints to the tubercles. The spines measure about 0.44 mm. in length, the proximal one of each pair is always bifurcated, with the branch (which may divide again) projecting proximally; the distal member of the pair is always straight and unbranched and leans forward (distally). Median to the pairs of spines there is always a low, somewhat triangular, flaring avicularium which possesses an incomplete hinge bar.

Within the deep zooecial chamber below the cryptocyst, a narrow horizontal shelf or ridge projects out from each lateral wall and unites around the distal wall. This shelf, which affords attachment for the occlusor muscles of the large operculum, is characteristic of the genus.

The ovicell is hyperstomial (external and resting on the proximal end of the succeeding zooecium), prominent, cucullate (hood-shaped and incomplete), and not closed by the operculum of the zooecium but having a separate membranous covering. The ovicell is only faintly marked by sculpturing; those markings present appear to be a matter of the degree of calcification. From the back side of the ovicell arises a tall, tubular avicularium which corresponds to the avicularium of a non-ovicelled zooecium.

Each lateral wall of the zooecium has a multi-porous rosette plate, and occasionally a third plate may be present on the distal wall.

The specimens in the present material are questionably designated as *C.*

galeata. They differ from Busk's brief description and figure in that the color of the zoarium is pink or orange, not purple, the proximal spines are bifurcated, the ovicell much more prominent, and the hinge bar of the avicularium is not complete. However, in the general aspects of Busk's figure and local specimens there is a reasonable resemblance. Upon examination of the figures and descriptions of this species by various authors, the writer finds that there is much confusion as to the concept of *galeata* (Busk). Waters (1898) stated that he had examined Busk's material and determined it to be the same as *C. annulus* (Manzoni). Waters' figure does not correspond to the Beaufort material. Canu and Bassler (1923) apparently confused two species under *C. galeata*; Osburn (1950) erected a new species, *C. californica*, to include one of the specimens figured by Canu and Bassler and designated the remaining figures as *C. patula* (Hincks).

Division III COILOSTEGA Levinsen, 1909

Family THALAMOPORELLIDAE Levinsen, 1909

Genus *Thalamporella* Hincks, 1887

Thalamoporella falcifera Hincks, 1880. (Fig. 34.)

Steganoporella rozieri form *falcifera* Hincks, 1880a: 380.
Thalamoporella falcifera, Osburn, 1914: 197; 1940: 380.

The zoarium encrusts floating algae (*Sargassum*). Zooecia are elongate quadrangular, about 0.60–0.75 mm. long and 0.32–0.35 mm. wide, thin-walled and fragile; the frontal is membranous. The cryptocyst is well developed, depressed for about half the length of the zooecium, then slanted upwards between two large perforations, the opesiules, to the proximal margin of the aperture. The cryptocyst is porous and minutely tuberculate. Opesiules are unequal in size, the larger one descending to the dorsal side and its insertion usually open, the smaller one generally inserting on the lateral wall, though it may reach the dorsal side where the insertion may be open or closed.

The zooecial aperture is somewhat longer than broad with a rounded sinus. The operculum occupies most of the aperture except the sinus. It is reinforced by a chitinous marginal sclerite and articulates with a small tooth on each side of the aperture, just above the sinus.

On each side of the aperture is an adoral area on which is located a rounded, calcified, hollow spine or tubercle.

The avicularium is interzooecial, with an elongate, narrow, curved mandible 0.28–0.30 mm. long.

All specimens were taken from *Sargassum* drift on Bogue Banks. The species is known in the Atlantic from the Tortugas Islands and Brazil.

Thalamoporella gothica var. *floridana* Osburn, 1940. (Fig. 35.)

Thalamoporella gothica var. *floridana* Osburn, 1940: 378.
Thalamoporella gothica var. *floridana*, Pearse and Williams, 1951: 137.

"Zoarium encrusting or erect. Adoral areas present, sometimes with tiny rounded tubercles. Opesia nearly circular with a rounded sinus without proximal shelf. Opesiules variable in size and form, one usually much smaller (sometimes wanting). Larger opesiule continued to the dorsal surface where its insertion is closed. Avicularia with pointed mandibles in the form of a gothic arch, the point raised. Avicularian cryptocyst incomplete, leaving a semicircular or semi-elliptical membranous area behind the mandibles. Ovicells not observed. Spicules in the form of calipers, large or small and intergrading" (Osburn).

Beaufort material agrees with Osburn's description except in the following features: adoral tubercles are always present in a well-developed condition; erect zoaria have not been observed; both opesiules are present as well as a few spicules in the form of open compasses.

The smooth cryptocyst of the zooecium is porous proximally up to the opesiules, with a few smaller pores scattered below the sinus of the aperture. The proximal pores of the avicularian cryptocyst are smaller than those of the zooecium.

The zooecia are variable in dimensions, ranging from 0.55 mm. to 0.60 mm. in length and 0.25 mm. to 0.35 mm. in width. The avicularian aperture is 0.35 mm. long and 0.18 mm. wide. These measurements agree closely with those of Osburn's specimens from Puerto Rico.

This species was found encrusting *Sargassum* collected from the jetties of Shackleford Banks and from Cape Lookout. Previously known from Florida and the West Indies north to the reefs at New River Inlet, North Carolina.

Family LUNULARIIDAE Levinsen, 1909 Genus *Discoporella* d'Orbigny, 1852

Discoporella umbellata (Defrance), 1823

Lunulites umbellata Defrance, 1823.
Cupularia umbellata, Smitt, 1873: 14.
? *Cupularia umbellata*, Verrill, 1878: 305.
Cupularia lowei, Osburn, 1914: 194.
Cupularia umbellata, Canu and Bassler, 1928: 64.
Discoporella umbellata, Osburn, 1940: 374; 1947: 18.

This species was not collected during the present survey but Verrill and Osburn have reported it here. Smitt records it from Cape Fear River.

The species resembles the following species, *D. doma*, but may be distinguished from it as follows: "Zoarium flatter than in *D. doma*, wider than high, umbrella-shaped. The cryptocyst forms almost a complete cover up to the opercular hinge by the fusion of its spinous processes, leaving usually a number of irregular holes besides the true opesiules" (Osburn, 1940: 374).

Discoporella doma (d'Orbigny), 1851. (Fig. 48, 49.)

Discoflustrellaria doma d'Orbigny, 1851: 561.
Cupularia doma, Smitt, 1873: 15.

Cupularia doma, Canu and Bassler, 1923: 77; 1928: 64.
Discoporella doma, Osburn, 1940: 374.

The zoarium is free, cup-shaped, with thick-walled zooecia facing out on convex surface; the dorsal concave surface is slightly roughened. The opesium is irregular in outline, bordered by about three variously shaped spines of the heavy cryptocyst. Two additional spines form condyles which articulate with the operculum. A vibraculum is situated at the distal end of each zooecium.

The single specimen collected was found on the beach at Bogue Banks. It measured 3.36 mm. in diameter. The mural rims were worn away so that the cryptocysts formed a smooth surface over the convex side of the zoarium, the zooecia boundaries being scarcely distinguishable.

This species differs from the preceding in that the cryptocyst spines do not coalesce so as to form a shelf up to the opercular hinge.

It is known on our coast from Florida, Straits of Florida, and Puerto Rico. It has also been found in Miocene deposits of Duplin marl at Wilmington, North Carolina.

Division V CELLULARINA Smitt, 1867

Family EPISTONIIDAE Gregory, 1903 Genus *Synnotum* Pieper, 1881

Synnotum aegyptiacum (Audouin), 1826. (Fig. 36.)

Loricaria aegyptiaca Audouin, 1826: 243.
Synnotum aviculare, Osburn, 1914: 191.
Synnotum aegyptiacum, Marcus, 1937: 58; 1938: 26.
Synnotum aegyptiacum, Osburn, 1940: 402; 1947: 25.

The zoarium is erect, branched and stolonate. The zooecia arise in pairs, back to back, with each pair beginning in a short tubular process; they are small and thinly calcified, with the frontal area occupying most of the length. In one or both of the distal corners of the zooecium is situated a sessile box-shaped avicularium. An occasional distal, pedunculate avicularium may be present on the dorsal side of a zooecium, this type being somewhat bulbous, with a very short hooked beak and mandible. Radicle fibers may also be present, in which case they also arise from the distal end of the zooecia.

There are no ovicells; the modified reproductive individuals, gonozooecia, are slightly enlarged.

Specimens were not collected during the present survey. However, material for examination from Cape Lookout was loaned by Dr. Osburn. The species is distributed on the Atlantic coast from Beaufort to Brazil.

Family BICELLARIELLIDAE Levinsen, 1909 Genus *Bugula* Oken, 1815

Bugula neritina (Linnaeus), 1758. (Fig. 37.)

Sertularia neritina Linnaeus, 1758: 815.
Acamarchis neritina, Verrill, 1878: 304.
Bugula neritina, Verrill, 1900: 593.

Bugula neritina, Osburn, 1914: 186; 1927: 126; 1940: 389; 1947: 22.
Bugula neritina, Marcus, 1937: 67.

The zoarium forms erect bushy tufts on most submerged substrates in shallow water. It is easily recognized by its reddish-brown or reddish-purple color and its phytoid appearance. It is the commonest bryozoan in the Beaufort area.

The zooecia are arranged biserially and alternately, all facing the same direction. There are no avicularia or spines; however, the frontal distal corners are sharply angular. The frontal area extends the entire length of the zooecium. Ovicells are globular and arise from the median distal corner of the zooecium so as to form a linear series, one above the other, in a fully mature colony.

The species is commonly distributed in warmer waters, reaching its northern limit on the coast of North Carolina and its southern limit in Brazil.

Bugula avicularia (Linnaeus), 1758. (Fig. 38–40.)

Sertularia avicularia Linnaeus, 1758: 809.
Bugula avicularia, Verrill, 1879a: 52; 1879b: 189; 1879c: 29.
Bugula avicularia, Osburn, 1912b: 226.
Bugula avicularia, Canu and Bassler, 1928: 41.
Bugula avicularia, McDougall, 1943: 339.

The zoarium is erect and branching, dull white in color. The zooecia are arranged biserially and alternately, each possessing three spines, one in each distal lateral corner and one in the distal median corner. The frontal area occupies most of the length of the zooecium. Midway along the lateral side of the zooecium is a large pedunculate, "bird's head" avicularium which is elongated and has a long slender beak gently curved to its tip. The character of the avicularium and its large size (0.25–0.30 mm.) distinguish this species from the two following. (See discussion of *B. californica*.)

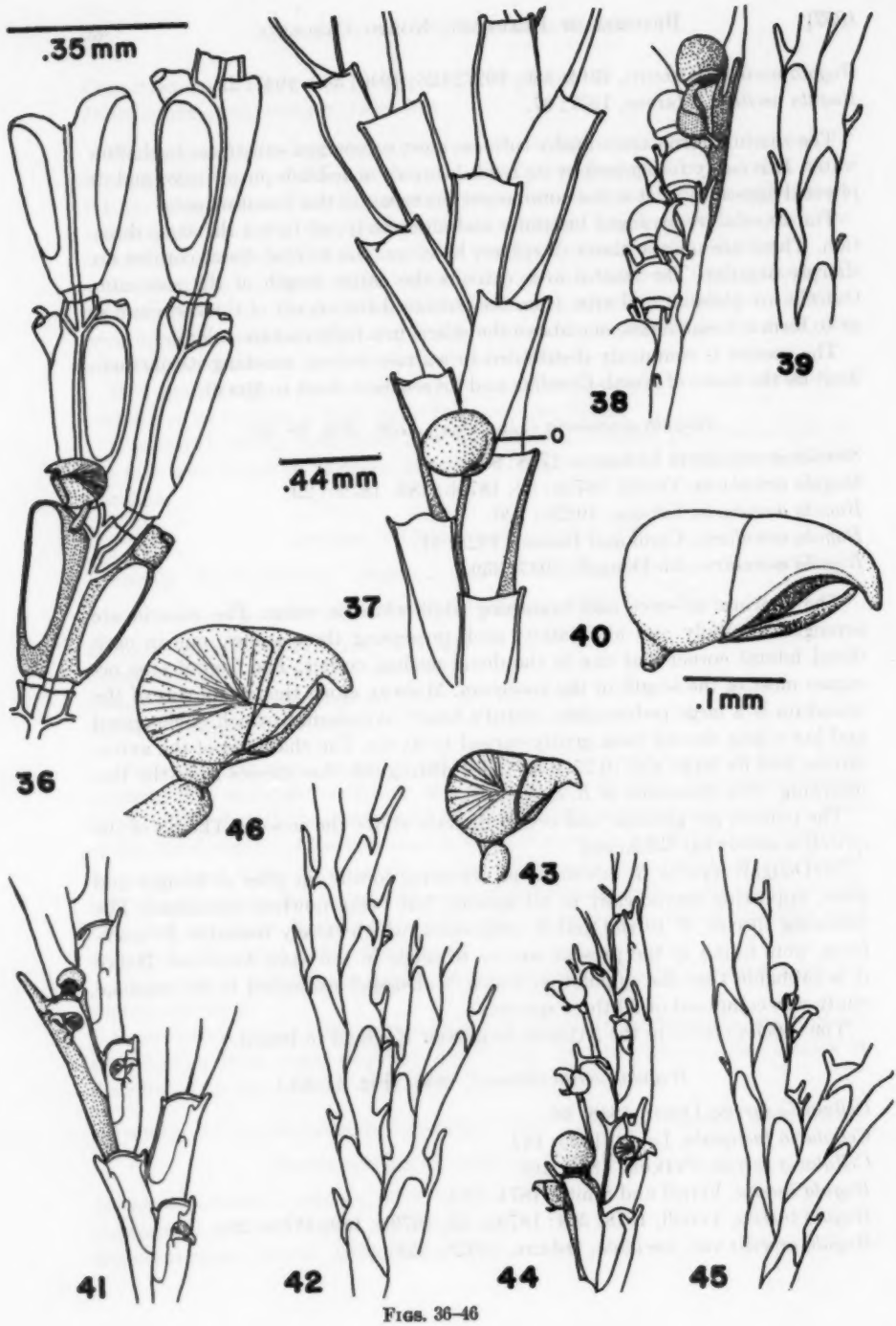
The ovicells are globular and center directly above the zooecia. The lip of the ovicell is somewhat thickened.

McDougall reports *B. avicularia* as occurring locally on piles of bridges and piers, appearing sporadically at all seasons, but being nowhere abundant. The following species, *B. turrita* and *B. californica*, which closely resemble *B. avicularia*, were found in the present survey to settle in the same localities. Hence it is probable that the population which McDougall examined in his seasonal study was composed of all three species.

The species occurs in the Atlantic from New England to Brazil.

Bugula turrita (Desor), 1848. (Fig. 41–43.)

Cellularia turrita Desor, 1848: 66.
Cellularia fastigiata, Leidy, 1855: 142.
Cellularia turrita, Perkins, 1869: 161.
Bugula turrita, Verrill and Smith, 1874: 712.
Bugula turrita, Verrill, 1878: 304; 1879a: 52; 1879b: 189; 1879c: 29.
Bugula gracilis var. *uncinata*, Osburn, 1912b: 224.



FIGS. 36–46

Bugula turrita, Osburn, 1912b: 225; 1944: 40; 1947: 23.
Bugula turrita, Marcus, 1937: 68.
Bugula turrita, Hutchins, 1945: 541.
Bugula turrita, Rogick and Coasdale, 1949: 51.

As in the other local representatives of *Bugula*, the zooecia are biserial and alternate. The frontal area extends about two-thirds of the length of the zooecium. A very short spine is usually present in each distal frontal corner (frequently only the distal angle is noticeable) and a larger, conical spine is present behind the outer spine. This latter spine may be quite elongated. A small pedunculate avicularium (0.15 mm. long) with a short decurved beak (0.05 mm.) is situated midway along the margin of the lateral wall. (See discussion of *B. californica*.)

The ovicells are globose and distinctively placed slightly to the median side of the zooecial axis and tilted toward the axis of the branch.

Ancestrulae are in the form of inverted cones, with the membranous area perpendicular to the axis of the zooecia and surrounded by five or more short spines. (See Marcus, 1938: 68–72, for description and figures.)

The growth form of this species is characterized by Osburn (1944) as one to three inches high, much branched, the branches bearing secondary whorled or spirally arranged branches which curl inward somewhat at their tips, giving each main branch a somewhat pyramidal form. This pattern was not distinguishable in local specimens nor was the size as large.

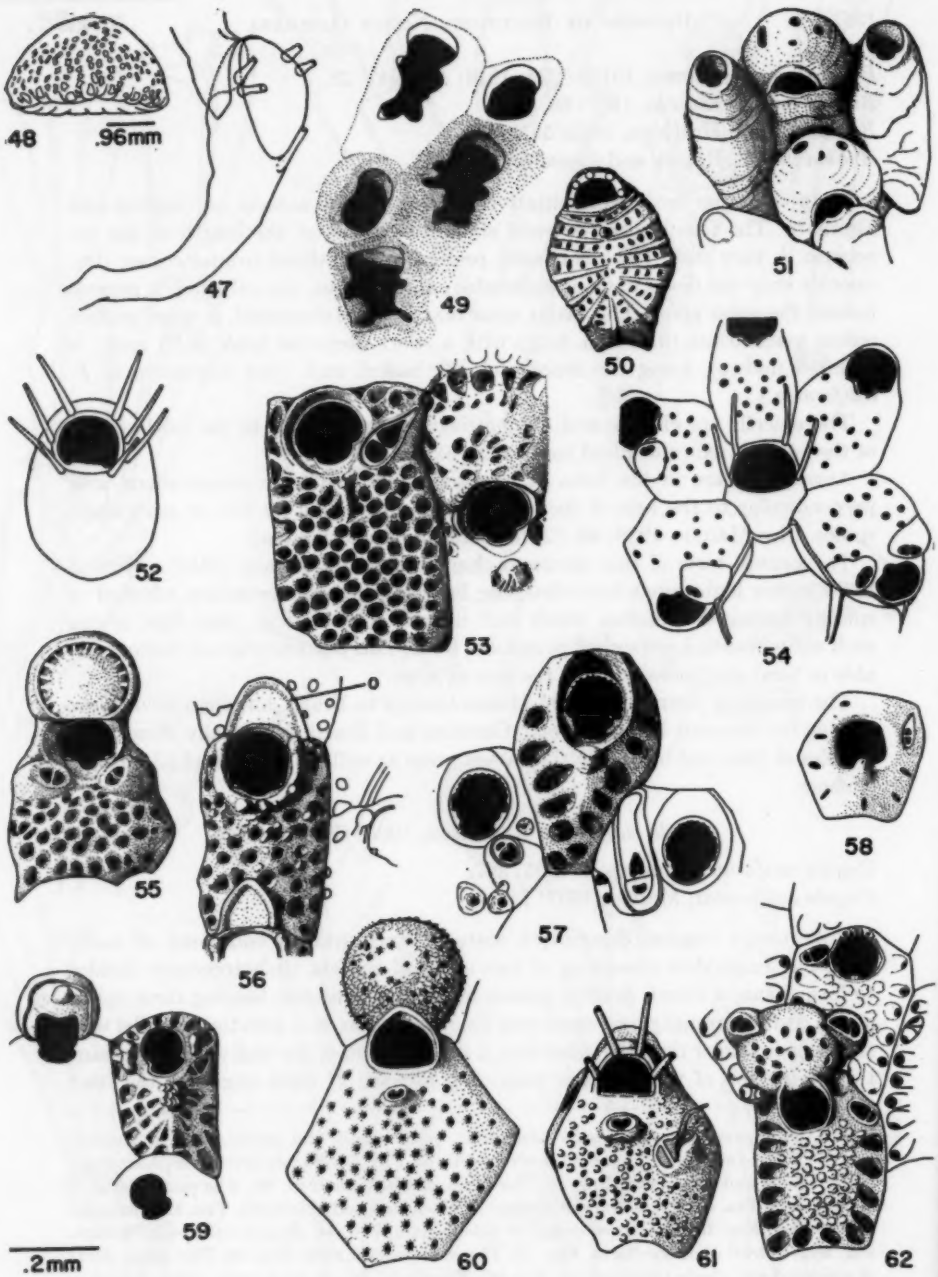
The species is distributed from Massachusetts to Brazil, although records are lacking for the coast between North Carolina and Brazil. It is locally distributed on piles of piers and bridges in the harbor areas as well as in depths of 13 fathoms offshore.

Bugula californica Robertson, 1905. (Fig. 44–47.)

Bugula californica Robertson, 1905: 267.
Bugula californica, Marcus, 1937: 71.

Robertson's original description states: "Each branch composed of many strap-like branchlets consisting of two series of zooecia, dichotomously divided to form a fan or frond. Zooecia narrowed below, elongated, bearing three spines at the distal extremity, one stout and long, extending in a direction parallel with the branch, longer than the other two, a continuation of the wall of the zooecium; two at the top of the aperture projecting forward at right angles to the front

FIG. 36. *Synnotum aegyptiacum* (Audouin), with sessile and pedunculate avicularia. FIG. 37. *Bugula neritina* (Linnaeus), with ovicell (o). FIG. 38. *Bugula avicularia* (Linnaeus), with ovicells and avicularia. FIG. 39. The same, dorsal view. FIG. 40. The same, detail of avicularium. FIG. 41. *Bugula turrita* (Desor), with ovicell and avicularia. FIG. 42. The same, dorsal view. FIG. 43. The same, detail of avicularium. FIG. 44. *Bugula californica* Robertson, with ovicell and avicularia. FIG. 45. The same, dorsal view. FIG. 46. The same, detail of avicularium. (Scale indicated for Fig. 36; Fig. 40, 43, 46 are same scale; other figures to scale of Fig. 37.)



FIGS. 47–62

surface. Aperture occupying more than two-thirds of the front of the zooecium. Avicularia large, pedunculate, situated near the top or not more than half the length of the zooecium below the top. Ooecia large, high, globose, extending above the lower margin of the aperture of the next upper zooecium. Rootlets developed on lower zooecia, springing from front or ventral surface of zooecium below the aperture."

There are two sizes of avicularia, those on the outer zooecial wall being 0.20–0.24 mm. long, those on inner zooecia just above a bifurcation being about 0.16–0.18 mm. long.

The ancestrula is shaped more or less like an inverted cone; the frontal area is ovoid and slanted, its margin provided with a median proximal spine and a pair of spines on each side in a disto-lateral position. The polypide possesses about 13 tentacles.

All of the "white" species of *Bugula* in the Beaufort area are provided with three spines at the distal end of the zooecia. Marcus states that the spines of *B. californica* are not simple prolongations of the aperture margin as in *B. turrita*, but are true spines, hollow and strongly calcified. Yet Robertson's description seems to indicate that the spines of *B. californica* are to be considered continuations of the aperture margin. The spines of all three of the species are hollow and calcified, in the opinion of the writer. The only general distinctions that can be made are that the spines of *B. avicularia* and *B. californica* are tubular and appear open at the ends whereas those of *B. turrita* appear conical and closed terminally; also, the two former species always have the three spines developed, while in the latter species the outer frontal spine is usually suppressed to a mere angle.

There appears to be a definite distinction, with little or no overlapping, on the basis of the size of the avicularia. It is doubtful whether this is a good distinction but from numerous specimens of all three species examined it is possible to separate them tentatively, according to avicularian length, as follows: *B. avicularia*, 0.25–0.30 mm.; *B. californica*, 0.20–0.24 mm.; *B. turrita*, 0.15–0.16 mm. Naturally, these size classes should not be considered alone, but may serve as aids along with the other specific features in arriving at a determination.

FIG. 47. *Bugula californica* Robertson, ancestrula. FIG. 48. Zoarium of *Discoporella doma* (d'Oribigny). FIG. 49. The same, detail of zooecia with 2 vibracula chambers; drawn from worn specimen. FIG. 50. *Colletosia radiata* (Moll). FIG. 51. *Hippothoa hyalina* (Linnaeus), with ovicells. FIG. 52. *Schizoporella unicornis* (Johnston), ancestrula with 8 spines. FIG. 53. The same, mature zooecium, avicularium, and ovicell. FIG. 54. *Schizoporella cornuta* (Gabb and Horn), ancestrula with 4 spines and first circuit of daughter zooecia. FIG. 55. The same, mature zooecium and ovicell. Note paired avicularia on mammillate processes. FIG. 56. *Hippodiplosia americana* (Verrill), with ovicell bud (o). FIG. 57. *Hippoporina contracta* (Waters), with 2 types of avicularia. FIG. 58. *Aimulosia uvulifera* (Osburn), with avicularium. FIG. 59. *Hippoporidra janthina* (Smitt), with ovicell and avicularium. FIG. 60. *Microporella ciliata* (Pallas), with ovicell. Note smooth and evenly perforated frontal wall characteristic of shallow water specimens. FIG. 61. The same, deep water form; note granulated, sparsely perforated frontal wall and setose avicularium mandible. FIG. 62. *Parasmittina trispinosa* (Johnston), with ovicell and avicularia; points of attachment of 3 oral spines shown in upper zooecium. (Fig. 48, scale indicated; Fig. 47, 49–62 are same scale.)

Bugula californica is locally distributed on piles of bridges and piers in the harbors, and on channel markers in Bogue Sound and Newport River. So far as it is known to the writer, Beaufort is the only place thus far reported where these three such closely resembling species of *Bugula* occur together. This is the second report of *B. californica* in the Atlantic and the first record north of Brazil. The species is regularly distributed along the Pacific coast from British Columbia to the Galapagos Islands.

Division VI CRIBRIMORPHA Harmer, 1926

Family CRIBRILINIDAE Hincks, 1880 Genus *Colletosia* Jullien, 1886

Colletosia radiata (Moll), 1803. (Fig. 50.)

Eschara radiata Moll, 1803: 63.
Cribrilina radiata, Smitt, 1873: 22.
Puellina radiata, Canu and Bassler, 1928: 73.
Colletosia radiata, Marcus, 1937: 73.
Puellina radiata, Osburn, 1940: 406.
Colletosia radiata, Osburn, 1947: 26.

The zoarium encrusts on shells and rocks. The zooecia are immediately distinctive in that the frontal surface possesses six or more pairs of radiating ridges or costules which are separated by a row of small lacunae or pores. A somewhat larger pore is usually present in a median position below the aperture. The aperture is semicircular, the proximal border being straight, and surrounded by five spines. Avicularia, when present, are vicarious, i.e., interzooecial in position.

Beaufort specimens were collected by Dr. Osburn on shell from the "fishing banks" (depth, 13 fathoms). None of the colonies possessed ovicells or avicularia.

The species is now known to be distributed on our coast from Beaufort, North Carolina, to Brazil.

Suborder ASCOPHORA Levinsen, 1909

Family HIPPOTHOIDAE Levinsen, 1909

Genus *Hippothoa* Lamouroux, 1821

Hippothoa hyalina (Linnaeus), 1767. (Fig. 51.)

Cellepora hyalina Linnaeus, 1767: 1286.
Mollia hyalina, Verrill and Smith, 1874: 713.
Hippothoa hyalina, Verrill, 1878: 305.
Schizoporella hyalina, Whiteaves, 1901: 100.
Hippothoa hyalina, Osburn, 1912a: 280; 1912b: 235; 1919: 609; 1932: 12; 1933: 33; 1944: 42.
Hippothoa hyalina, Marcus, 1937: 79.
Hippothoa hyalina, Hutchins, 1945: 542.
Hippothoa hyalina, Rogick and Croasdale, 1949: 57.
Hippothoa hyalina, Pearse and Williams, 1951: 137.

The zoarium is encrusting, glistening white or nearly transparent (in younger

stages). The zooecia are more or less elongate, subcylindrical, narrowed proximally, and distinctly separated from one another, the margins containing areolated spaces. The frontal wall is glossy, imperforate and transversely lined by growth ridges. A small umbonate process may be present on top of the most inflated portion of the zooecium, i.e., just proximal to the aperture. The aperture is rounded with a shallow, broad sinus on the proximal border.

The conspicuous ovicells are globose and perforated by a few scattered, irregular pores. The fertile zooecia are usually shallower and shorter than the infertile ones.

Though reported by several authors to settle on almost any substrate, the species is to be found in the Beaufort area only on the larger algae, particularly the browns such as *Sargassum* and *Zonaria*.

The species is cosmopolitan.

Family SCHIZOPORELLIDAE Jullien, 1903 (in part)

Genus *Schizoporella* Hincks, 1887

Schizoporella unicornis (Johnston), 1847. (Fig. 52, 53.)

Lepralia unicornis Johnston, 1847: 320.
Lepralia variolosa, Desor, 1848: 66.
Escharina variabilis Leidy, 1855: 10.
Hippothoa isabelleana Smitt, 1873: 44.
Escharella variabilis, Verrill and Smith, 1874: 713.
Hippothoa variabilis, Verrill, 1875b: 41; 1878: 305.
Hippothoa reversa Verrill, 1875b: 41.
Schizoporella unicornis, Osburn, 1912b: 236; 1914: 205; 1940: 419; 1944: 43; 1947: 28.
Schizopodrella pungens Canu and Bassler, 1928: 97.
Schizopodrella isabelleana, Canu and Bassler, 1928: 97.
Schizopodrella unicornis, Osburn, 1932b: 443; 1933: 38.
Schizoporella unicornis, Pelluet and Hayes, 1936: 157.
Schizoporella unicornis, Marcus, 1937: 83.
Schizoporella pungens, Marcus, 1937: 86.
Schizoporella unicornis, Hutchins, 1945: 542.
Schizoporella unicornis, Rogick and Croasdale, 1949: 66.
Schizoporella unicornis, Pearse and Williams, 1951: 137.

The zoarium encrusts on practically all firm substrates such as rocks, shells, wood, algal thalli, decapod and king crab carapaces, etc. The color is variable, red-orange being more common than white, pink, or orange. Older colonies are usually multilaminate with as many as twenty layers or more.

The zooecia are usually quadrangular in outline, but the shape is quite variable and may appear as polygonal or oval in young colonies. Zooecia are arranged radially about the ancestrula; however, in multilaminate colonies orientation is lacking. The frontal is a tremocyst, i.e., a porous secondary calcified layer, with rather large perforations, much thickened in older zooecia. An umbo is usually

present below the aperture. The aperture is rounded distally with a rounded sinus on the proximal border. A smooth, thin peristome is present. An avicularium with a pointed mandible is usually situated to one side of the aperture, the mandible pointing forward. The avicularia may be paired, one on each side of the aperture, or scattered irregularly without orientation, variously elevated, or absent entirely from considerable portions of the zoarium. In a series of young colonies studied, avicularia usually first appeared in the sixth or seventh circle of zooecia.

The ovicells are globular, perforated irregularly, and sometimes crowned by an umbonate process.

The zooecia are 0.35–0.66 mm. long and 0.24–0.55 mm. wide, averaging toward the larger dimensions; aperture length and width is 0.13–0.15 mm. and 0.13 mm. respectively; avicularia are quite variable in size.

The ancestrula is ovoid, 0.38 mm. long and 0.30 mm. wide, with a thin imperforate frontal and eight long spines surrounding the aperture. The aperture is similar in shape to those of the daughter zooecia but lacks a sinus.

The species is cosmopolitan and is one of the most common of the encrusting orms in the Beaufort area.

Schizoporella cornuta (Gabb and Horn), 1862. (Fig. 54, 55.)

Heptescharellina cornuta Gabb and Horn, 1862: 147
Hippothoa biaperta, Smitt, 1873: 46.
Hippothoa biaperta, Verrill, 1875b: 41; 1878: 305.
? *Escharina biaperta*, Verrill, 1879b: 193.
Schizoporella biaperta, Osburn, 1912b: 237; 1914: 207; 1933: 39.
Stephanosella biaperta, Canu and Bassler, 1923: 99.
? *Schizoporella* (*Stephanosella*) *biaperta*, Osburn 1947: 29.
Schizoporella biaperta, Rogick and Croasdale, 1949: 66.

The zoarium is white to brownish in color, encrusting on shells. The zooecia are smaller than those of the preceding species, 0.35–0.48 mm. long and 0.25–0.33 mm. wide. The frontal is a tremocyst, perforated irregularly, and usually bears a pair of elliptical sessile avicularia, each located on a mammillate process on each side of the aperture. Occasionally one or both of the avicularia are absent on some zooecia. The aperture is rounded distally and has a sinus, somewhat V-shaped, on the proximal-border; a lateral hinge denticle (cardelle) is present on each side of the top of the sinus. The aperture is 0.10–0.12 mm. in length (to bottom of sinus) and 0.10–0.13 mm. in width.

The ovicell is prominent, globular, and only partially embedded even in advanced calcification, not closed by the operculum; imperforate, its frontal surface radially grooved, the secondary cover incomplete and exposing a rounded area on the top, appearing to have a peripheral row of pores but these are merely the bottoms of the grooves at the edge of the secondary cover (Osburn, 1952: 320–321).

The ancestrula is ovoid and imperforate, about 0.25 mm. long and 0.18 mm.

wide, with four long erect spines surrounding the aperture. The aperture lacks a sinus.

Schizoporella cornuta can be distinguished from *S. unicornis* by its smaller size, the shape of the avicularian mandibles, the mammillate processes, and the appearance of the ovicells.

The known range on the Atlantic coast must remain incomplete for the present since the species has been confused with *Stephanosella biaperta* (Michelin) which it closely resembles. However the latter has an olocyst (imperforate frontal) with only lateral areolar pores. On the basis of published figures the range is at least from Woods Hole to Florida.

Schizoporella floridana Osburn, 1914

Schizoporella floridana Osburn, 1914: 205.
Schizopodrella floridana, Osburn, 1927: 126.
Schizopodrella floridana, Canu and Bassler, 1923: 106; 1928: 93.
Schizoporella floridana, Osborn, 1940: 422; 1947: 29.
Schizoporella floridana, Pearse and Williams, 1951: 137.

This species is very much like *S. unicornis* but differs in the following details: the avicularia of young or marginal zooecia are usually placed lateral or distal to the aperture, the mandibles well-curved toward the zooecial axis so as to conform with the aperture margin; large vicarious avicularia with straight, pointed mandibles occur on hemispherical chambers as large as the zooecia in multilaminate colonies; the ovicell is slightly wider than long and minutely perforated.

The zoarium is encrusting, usually occurring in multilaminate masses. The mandible of the oral avicularium may be straight and directed forward, laterally or backwards, and sometimes the avicularium may be proximal to the aperture.

The species has not been found as yet at Beaufort but is known to occur off New River Inlet and in Miocene deposits near Wilmington, North Carolina. It is to be expected in reef habitats offshore from Beaufort, possibly reaching its northern limit here.

Genus *Hippodiplosia* Canu, 1916

Hippodiplosia americana (Verrill), 1875. (Fig. 56.)

Lepralia americana Verrill, 1875a: 415.
Lepralia americana Verrill, 1875b: 42; 1878: 305.
Lepralia pallasiana, Davenport, 1891: 47.
Lepralia americana, Osburn, 1912b: 241.
Hippodiplosia americana, Osburn, 1933: 40.
Hippodiplosia americana, Marcus, 1937: 101.
Hippodiplosia americana, Hutchins, 1945: 543.

The zoarium encrusts shells. Zooecia may be quadrangular or somewhat hexagonal, frequently separated by a low, raised border. They are of moderate

size, about 0.45–0.55 mm. in length and 0.30–0.35 mm. in width. The frontal is a tremocyst with large pores and may be thickened into a ridge or umbo along the proximal border of the peristome; roughened in older zooecia. The aperture is rounded, 0.13–0.15 mm. long and 0.12–0.13 mm. wide, broadly arcuate on the proximal border just below the cardelles. The peristome is low and thin. Avicularia are wanting in the local specimens examined. No mature ovicells were observed but some specimens possessed buds of these structures.

The species is found uncommonly in Bogue Sound. Along the Atlantic coast it has been reported from Maine to North Carolina and from Brazil.

Family HIPPOPORINIDAE Osburn, 1952 Genus *Hippoporina* Neviani, 1895

Hippoporina contracta (Waters), 1899. (Fig. 57.)

Lepralia contracta Waters, 1899: 11.
Lepralia serrata Osburn, 1912b: 242.
Lepralia contracta var. *serrata* Osburn, 1914: 211.
Perigastrella contracta, Canu and Bassler, 1920: 576.
Perigastrella contracta, Marcus, 1937: 98.
Hippoporina contracta, Osburn, 1940: 428; 1947: 33.
Hippoporina contracta, Hutchins, 1945: 543.
Hippoporina contracta, Rogick and Croasdale, 1949: 57.
Hippoporina contracta, Pearse and Williams, 1951: 137.

The zoarium forms a thick, white, glossy crust on shells. Zooecia are more or less hexagonal, about 0.45 mm. long and 0.35 mm. wide, and possess a non-perforated, extremely thick and roughened frontal which is surrounded by rather large marginal areolae. The aperture is rounded and slightly elongated, 0.15 mm. long and 0.13 mm. wide, characteristically beaded around the margin distal to the cardelles, with a rather deep, broadly arched sinus on the proximal border; the cardelles are distinctively bifid. Heavy calcification of the frontal forms a secondary peristome and results in the aperture's being deeply submerged from the surface. The avicularia are variously shaped, oval, spatulate, to very elongate, and may or may not be mounted on low, mammillate processes.

No ovicells were observed in local specimens, nor were there any spines around the aperture as reported to occur in less heavily calcified zooecia.

One specimen was collected on a shell dredged from 40 feet in depth offshore just east of Beaufort Inlet. Other specimens that were examined were collected by Dr. Osburn from the "fishing banks" in a depth of 13 fathoms. The species is distributed on the Atlantic coast from Woods Hole to Brazil.

Genus *Aimulosia* Jullien, 1888

Aimulosia wulifera (Osburn), 1914. (Fig. 58.)

Lepralia wulifera Osburn, 1914: 210.
Lepralia wulifera Osburn, 1940: 427.
Aimulosia wulifera Osburn, 1947: 35.

The zoarium is encrusting, composed of small ovate or hexagonal zooecia which

are about 0.30–0.35 mm. in length and 0.30 mm. in width. The frontal is a smooth, porcelain-like pleurocyst which is thickened and highly arched so as to obscure the peristome and somewhat imbed the aperture; areolar pores are scattered along the margin and are separated by short costae. The aperture is straight-sided, rounded distally, broadly arcuate or nearly straight proximally, about 0.1 mm. long and 0.08 mm. wide; young specimens have six marginal spines around the aperture. An umbo or rostrum projects over the aperture, its tip rounded or trifid. Small, pointed avicularia may be present in various positions proximal or lateral to the aperture.

No ovicells or spines were observed in the local material, but locations of a few of the spines were still evident in some. The trifid condition of the umbo was not seen. A single avicularium was observed on most specimens, its position being lateral to the aperture.

The specimens were collected on shell offshore from Beaufort Inlet in 40 feet and one zoarium was taken from a skate egg case found on Bogue Banks.

The species has previously been reported in the Atlantic from the Tortugas Islands, Puerto Rico, and the West Indies.

Genus *Hippoporidra* Canu and Bassler, 1927

Hippoporidra janthina (Smitt), 1873. (Fig. 59.)

Lepralia edax form *janthina* Smitt, 1873: 63.
Lepralia janthina, Osburn, 1914: 213.
Hippotrema janthina, Canu and Bassler, 1928: 141.
Hippotrema janthina, Osburn, 1940: 454; 1947: 43.
Hippoporidra janthina, Osburn, 1952: 355.

The zoarium is encrusting, forming thick, rough, tuberculate layers on gastropod shells. Young zooecia are white, becoming a dark violet with increasing age. The zooecia are 0.35–0.45 mm. in length and 0.25 mm. in width. The frontal of young stages is smooth and perforated only around the margins by areolar pores; much thickened as a pleurocyst in older zooecia, strongly ribbed, the costal ridges arising between the areolar pores and uniting below the aperture to form an irregular, massive umbo. The frontal has the appearance of a tremocyst but Osburn (1952), in explaining its nature, states that it is really a pleurocyst which arises as a series of costal ridges between the pores and spreads upward to the aperture, carrying the openings of the pores upward at the same time, resulting in a perforated appearance. The ridges may be smooth or nodular; occasionally a large protuberance similar to the umbo may be present on each side of the aperture. The aperture is divided into two portions by a pair of strong cardelles, the anter or distal portion is circular and the poster or proximal portion is a deep, broad arch. Aperture length is about 0.10 mm. and the width is 0.08 mm. The peristome is thin and spineless, generally obscured in advanced calcification of the frontal. A small avicularium with a pointed mandible is usually present, located on a prominence near the aperture. An occasional large interzooecial avicularium may be found.

The ovicells are prominent, not closed by the operculum, and have a somewhat semicircular area surrounded by a fold which extends down either side of the opening. A small tubercle is usually present in the center of the area.

One local specimen was encrusting a *Nassarius obsoleta* shell occupied by a hermit crab, *Pagurus annulipes*. It was collected on the sound side of Shackleford Banks. Another specimen from Newport River formed an extensive growth on a gastropod shell inhabited by *Pagurus longicarpus*. The species has been previously reported in the Atlantic from the Gulf of Mexico and various localities in the West Indies.

Family MICROPORELLIDAE Hincks, 1880 Genus *Microporella* Hincks, 1877

Microporella ciliata (Pallas), 1766. (Fig. 60, 61.)

Eschara ciliata Pallas, 1766: 38.
Lepralia ciliata, Packard, 1867: 270.
Porellina ciliata, Smitt, 1873: 26.
Porellina ciliata, Verrill, 1879c: 29.
Microporella ciliata, Osburn, 1912a: 279; 1912b: 233; 1914: 208; 1923: 10D; 1927: 129; 1932a: 13; 1932b: 443; 1940: 432; 1944: 45; 1947: 35.
Microporella ciliata, Canu and Bassler, 1923: 119; 1928: 110.
Microporella ciliata, Marcus, 1937: 110.
Microporella ciliata, Hutchins, 1945: 543.
Microporella ciliata, Rogick and Croasdale, 1949: 63.
Microporella ciliata, Pearse and Williams, 1951: 137.

The zoarium is composed of translucent and silvery zooecia (opaque and white in incinerated or "calcined" specimens), encrusting shells and rocks, rarely larger brown algae such as *Zonaria*. Considerable variation in size, shape and anatomical features occurs even in the same colony. The zooecia may be ovate, quadrangular or hexagonal; they are about 0.40–0.55 mm. long, 0.25–0.50 mm. wide, and frequently separated by large pores. The frontal is a tremocyst, slightly curved to gibbous, smooth and evenly perforated or granular and sparsely punctured. The aperture is semicircular, the proximal border straight and usually finely serrate; it is 0.08–0.10 mm. long, and 0.09–0.13 mm. wide. The peristome is low and smooth and is bordered laterally and distally by four to seven spines. Proximal to the aperture, at a variable distance, is a semilunate or oval ascopore which has minute spicules projecting into it. The ascopore is usually slightly elevated, sometimes surrounded by a flattened area which may in turn be bounded by a low ridge. Frequently the proximal portion of the ridge may be raised into a small umbonate process.

Usually a small avicularium is situated lateral and slightly proximal to the ascopore, and most often points laterally. The mandible may vary from short and triangular to long and setose, the latter type bearing two hooks on the inner surface.

The ovicell is globose, smooth, slightly ribbed, or granulated, and may be sparsely perforated. A thin collar is usually present extending from the proximal

corners of the aperture and around the margin of the ovicell directly behind the aperture.

Specimens from the shallow waters of the sounds are smooth-surfaced and evenly perforated (Fig. 60). Those dredged from forty feet off Beaufort Inlet are granulated, sparsely perforated, and have setose avicularium mandibles (Fig. 61).

The species is distributed on the Atlantic coast from Labrador to Brazil.

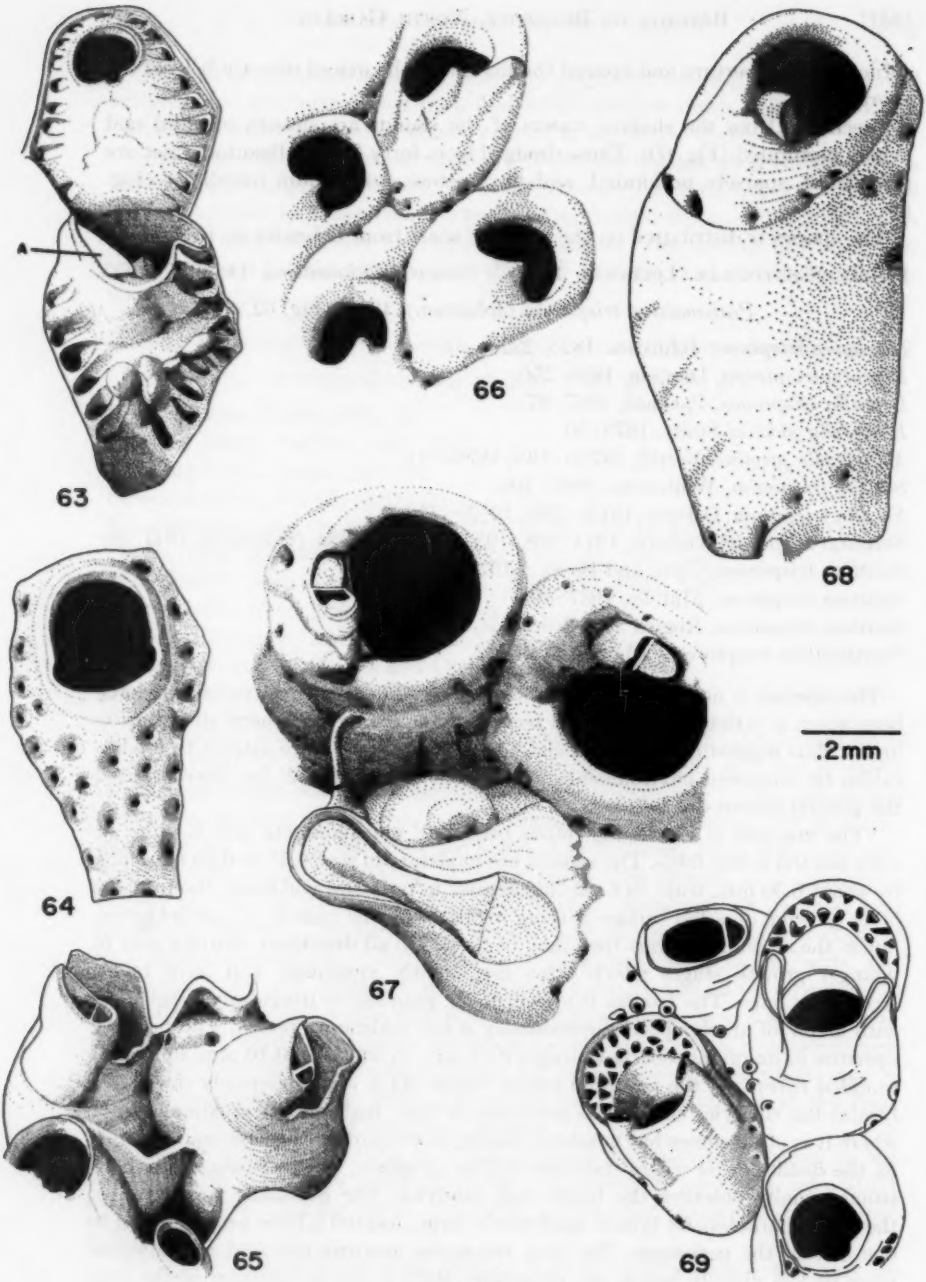
Family SMITTINIDAE Levinsen, 1909 Genus *Parasmittina* Osburn, 1952

Parasmittina trispinosa (Johnston), 1825. (Fig. 62.)

Discopora trispinosa Johnston, 1825: 222.
Lepralia trispinosa, Dawson, 1859: 256.
Lepralia trispinosa, Packard, 1867: 67.
Escharella jacotini Smitt, 1873: 59.
Mucronella jacotini, Verrill, 1879b: 195; 1879c: 31.
Smittia trispinosa, Whiteaves, 1901: 106.
Smittia trispinosa, Osburn, 1912a: 286; 1912b: 246.
Smittina trispinosa, Osburn, 1914: 208; 1933: 45; 1940: 434 (varieties); 1947: 36.
Smittina trispinosa, Canu and Bassler, 1923: 143.
Smittina trispinosa, Marcus, 1937: 102.
Smittina trispinosa, Rogick and Croasdale, 1949: 67.
Parasmittina trispinosa, Osburn, 1952: 412.

This species is noted for its great variability. The recurrent variations have been given a variety of names and seem to have few or no general distribution limits, thus suggesting that most characters of the species are subject to modification by numerous environmental conditions. Osburn (1952) has characterized the general features as follows:

"The zoarium is encrusting, often becoming multilaminate and nodular or even erected in low folds. The zooecia are moderate in size, 0.45 to 0.60 mm. long by about 0.30 mm. wide, but varying greatly in both size and form; the primary layer growing on a flat surface is quite regular with the zooecia in parallel series, but in the secondary layers they may be turned in all directions: distinct only in younger growth stages which often are slightly ventricose and have raised separating lines. The frontal is a pleurocyst, granular or irregularly roughened, with a row of areolar pores (occasionally a few additional pores). The primary aperture in marginal zooecia averages 0.11 mm. in width by 0.10 mm. in length, rounded except on the proximal border where there is a moderately developed lyrula; the condyles small. The peristome is thin, high on the proximal border where it is often somewhat notched, sloping downward on the sides and wanting on the distal border where there are 3 (2 to 4) spines; the overhang of the peristome usually obscures the lyrula and condyles. The avicularia are variable; the most characteristic type is moderately large, located a little proximal and to one side of the peristome. The long triangular rostrum elevated and directed more or less distally beside the peristome, there is much variation in the size;



FIGS. 63–69

frequently there are other avicularia, varying in size and form distributed irregularly over the frontal.

Ovicell prominent, the frontal surface usually a little flattened, with moderately large pores that vary in size and form; width 0.26 mm.; in full calcification the front often becomes rough and the ovicell much embedded."

Living colonies are pinkish, becoming yellow when dead if the ectocyst is intact. Most local specimens have the peristome raised as a lappet-like process on each side of the secondary orifice and possess the oval type of avicularium characteristic of the variety *nitida* (Verrill). These may also have ovicells with raised borders surrounding finely perforated frontal areas. Others have the rather large areolar pores and spatulate avicularia common to the variety *spathulata* (Smitt).

For the present, all of the variety forms are lumped together herein without any special nomenclatorial status. The literature listed above refers only to those papers reporting the "typical" form of the species, though many of them report numerous variety forms.

The species is one of the commonest encrusting species in the Beaufort area and is widely distributed from Newport River and the sounds to offshore.

Parasmittina trispinosa with all of its varieties is a cosmopolitan species.

Family RETEPORIDAE Smitt, 1867 Genus *Rhynchozoon* Hincks, 1895

Rhynchozoon rostratum (Busk), 1856. (Fig. 63.)

Lepralia rostrata Busk, 1856: 178.
Cellepora verruculata Smitt, 1873: 50.
Cellepora verruculata, Osburn, 1914: 214.
Rhynchozoon verruculatum, Canu and Bassler, 1923: 157.
Rhynchozoon verruculatum, Marcus, 1939: 153.
Rhynchozoon verruculatum, Osburn, 1940: 444.

The zoarium encrusts shells, forming rough, irregular masses. Advanced calcification so obscures and modifies the general zooecial features that practically no two zooecia look alike. Young or marginal zooecia are perhaps best to characterize. These are more or less ovate to hexagonal, slightly inflated and show early tendencies toward heavy calcification in that the frontal becomes much thickened marginally even before calcification is complete in the median line; they are distinctly marked off from one another by deep grooves, or occasionally by raised borders. Areolar pores separated by short low costules are present around the margin. The zooecia are of moderate size, about 0.45–0.55 mm. long

FIG. 63. *Rhynchozoon rostratum* (Busk), with avicularium (A). Upper individual is a young marginal zooecium. FIG. 64. *Cryptosula pallasiana* (Moll). FIG. 65. *Schizmopora dichotoma* (Hincks), with avicularia on the sides of raised umbos. FIG. 66. *Schizmopora margaritacea* (Pourtales). FIG. 67. *Holoporella magnifica* Osburn, with small oral avicularia and a large interzooecial avicularium. (Specimen from Bermuda, R. C. Osburn, collector.) FIG. 68. The same, marginal zooecium. FIG. 69. *Costazia costazii* (Audouin), with ovicells and paired peristomial avicularia; large interzooecial avicularium at upper left. (All the same scale.)

and 0.30 to 0.40 mm. wide. The primary aperture is slightly wider than long, averaging about 0.13 mm. wide by 0.11 mm. long, with a proximal sinus and a beaded vestibular arch. The primary peristome is thin and without spines. As calcification proceeds, a thin (later much thickened) secondary peristome develops as a somewhat flaring collar with one or two proximal notches. Adjacent to the peristomial notches and to one side of the median line a large, bulbous avicularium chamber develops, occupying more than half of the frontal width, the rostrum elevated above the aperture and directed laterally. Both the mandible and rostrum are strongly hooked. Ultimately the suboral avicularium becomes submerged in the peristome. Continued thickening of the frontal results in the scattering of strong ridges and tubercles over the surface.

Frontal avicularia similar to the suboral ones are to be found on older zooecia. These usually have pointed mandibles and may be variously oriented; not more than one per zooecium.

Ovicells were not observed in local material. The specimens examined were collected by Dr. Osburn from the "fishing banks" in thirteen fathoms.

The species is distributed in the Atlantic from Massachusetts to Brazil.

Family CHEILOPORINIDAE Bassler, 1936

Genus *Cryptosula* Canu and Bassler, 1925

Cryptosula pallasiana (Moll), 1803. (Fig. 64.)

Eschara pallasiana Moll, 1803: 57.
Escharina pediostoma Leidy, 1855: 141.
? *Lepralia pallasiana*, Verrill and Smith, 1874: 713.
Lepralia americana Verrill, 1875a: 414 (in part).
Lepralia pallasiana, Cornish, 1907: 77.
Lepralia pallasiana, Osburn, 1912b; 240.
Cryptosula pallasiana, Osburn, 1933: 43.
Cryptosula passasiana, Hutchins, 1945: 543.
Cryptosula pallasiana, Rogick and Croasdale, 1949: 55.

The zoarium encrusts shells and practically any other firm substrate. The zooecia are hexagonal or coffin-shaped, moderately large, about 0.60–0.70 mm. long and 0.40 mm. wide. The aperture is somewhat bell-shaped, the poster being broadly arcuate and wider and shallower than the anter, the sides nearly parallel; it is about 0.21–0.24 mm. long and 0.18–0.20 mm. wide; the cardelles are small. The peristome is raised and not fused with the frontal. The frontal is a tremocyst with large depressed pores. There are no ovicells. Small avicularia have been occasionally reported for this species, but none were observed on Beaufort specimens.

Locally, the species is relatively common in the sounds and estuaries. It is distributed along the Atlantic coast from Nova Scotia to northern Florida.

Family CELLEPORIDAE Busk, 1852 Genus *Schizmopora* MacGillivray, 1888

Schizmopora dichotoma (Hincks), 1862. (Fig. 65.)

Cellepora dichotoma Hincks, 1862: 305.
Cellepora avicularis Smitt, 1873: 53.

? *Cellepora avicularis*, Verrill, 1878: 305; 1901a: 54.
Cellepora dichotoma, Osburn, 1914: 214.
Schismopora dichotoma, Canu and Bassler, 1928: 149.
Cellepora dichotoma, Marcus, 1938: 46.
Schizmopora dichotoma, Osburn, 1940: 460; 1947: 43.
Cellepora dichotoma, Rogick and Croasdale, 1949: 53.
Schizmopora dichotoma, Pearse and Williams, 1951: 138.

The original description by Hincks is as follows: "Polyzarium slender, narrowed towards the base, dichotomously branched; branches cylindrical, tapering towards the extremities, pointed; cells ovate, ventricose, smooth; orifice orbicular above, slightly produced below, in front of it a short and tumid rostrum, with a small avicularium on one side of it, near the top; ovicell globose, silvery, covered in front with punctures, the margins of which raised; occasionally a spatulate avicularium on one side of the orifice; numerous minute subcircular avicularia distributed amongst the cells. The surface of the polyzoary is pierced by circular orifices, which occupy the intercellular spaces."

Rogick has better summarized the characteristics as: (1) peristome with a sinus next to a raised umbo on the side of which is an avicularium facing the sinus; (2) aperture rounded, with postral sinus; (3) ovicell with pores, rounded and somewhat flattened; and (4) a few small pores (areolae) around the frontal wall of the zooecium.

Beaufort specimens were collected by Dr. Osburn at thirteen fathoms on the "fishing banks." The material is quite fragmentary, composed of masses of semi-erect zooecia. Only a few ovicells are present and none of these are intact.

The species is distributed along the coast from New England to Brazil.

Schizmopora margaritacea (Pourtales), 1867. (Fig. 66.)

Vincularia margaritacea Pourtales, 1867: 110.
Cellepora margaritacea, Smitt, 1873: 53.
Schizmopora margaritacea, Osburn, 1940: 460.

The zoarium grows erect from an encrusting base, branching irregularly, generally at a large angle. The zooecia are evenly distributed on all sides; they are oval, smooth, and rather indistinctly separated, about 0.55 mm. in length and 0.30 to 0.35 mm. in width; the margins contain a few shallow pores. The aperture is rounded, 0.12 mm. in width, with a broad, shallow sinus. A small avicularium is situated on the distal side of a low umbonate process which is placed proximally to the aperture and to one side of it. Advanced calcification generally obscures the primary aperture revealing only a wider secondary orifice which may enclose the avicularium. No oral spines are evident on the material at hand, but Smitt reports four and Osburn (1952: 494) two.

The ovicell is globose and cribriform, being evenly perforated.

Local specimens were collected by Dr. Osburn from the "fishing banks" (13 fathoms). Only several tiny fragments were available for examination, none showing the growth form of the zoarium.

The species is reported in the Atlantic from Beaufort, Sand Key, Florida, and off Havana, Cuba.

Genus *Holoporella* Waters, 1909

Holoporella magnifica Osburn, 1914. (Fig. 67, 68.)

Holoporella magnifica Osburn, 1914: 216.
Holoporella magnifica, Canu and Bassler, 1928: 143.
Holoporella magnifica, Osburn, 1940: 455; 1947: 44.
Holoporella magnifica, Pearse and Williams, 1951: 138.

The zoarium is encrusting, composed of large, dark brown zooecia which have very large apertures. The zooecia are ovate, inflated in young stages, 0.65–0.85 mm. in length and 0.55–0.85 mm. in width, procumbent at the growing edge, erect and irregular at the center of the colony; a few scattered marginal pores are present as well as occasional pores or pits around the base of the peristome. The aperture is distinctively large, 0.28 mm. wide, its shape a little more than a semicircle with a straight proximal border. The peristome is very thick and broad, raised into a heavy projecting rostrum to one side of the proximal border of the aperture, and contains on its median side a large avicularium with a rounded mandible which closes in an upright position. There are large spatulate, vicarious avicularia scattered among the zooecia, these falling into two size classes, 0.40 mm. and 0.20–0.28 mm. in length. The ovicell is a wide open hood.

The species has been reported by Osburn from the "fishing banks" but it was not collected during the present study. Pearse and Williams reported it on the reefs at New River Inlet in 15 to 20 feet. It has been reported in the Atlantic from North Carolina, Tortugas Islands, Biscayne Key, Puerto Rico, Bermuda, and the Gulf of Mexico.

Genus *Costazia* Neviani, 1895

Costazia costazii (Audouin), 1826. (Fig. 69.)

Cellepora costazii Audouin, 1826: 237.
? *Siniopella costazii*, Marcus, 1937: 121.
Costazia costazii, Osburn, 1940: 461.

The zoarium encrusts algae, particularly the firmer browns such as *Sargassum* and *Zonaria*, forming small, rough and nodular patches. The zooecia are of moderate size, 0.55–0.65 mm. long and about 0.30 mm. wide, glabrous, and somewhat inflated, perforated only by scattered marginal pores. The aperture is almost semicircular, the proximal border only slightly arched and with a rounded sinus. The aperture length (to bottom of sinus) is about 0.14 mm. and the width is 0.13–0.14 mm. A high peristome usually obscures the aperture. The peristome forms from the frontal as a thin elevated sheet which folds back on itself at the lateral corners, thus forming a tall tube on each side which bears at the tip an ovate avicularium, the two facing each other across the aperture. The peristome is developed around the distal border of the orifice as a broad lip which extends

across the ovicell in fertile zooecia. The ovicell is somewhat immersed, broader than long, and possesses a crescent-shaped area with angular pores arranged in a radiate manner. Marginal ovicells have a more semicircular area. Vicarious spatulate avicularia of varying sizes are scattered about in the colonies.

Beaufort specimens differ from the description given by Osburn (1952: 506) in that (1) the frontal is not roughened; (2) the aperture is not noticeably longer than broad; and (3) the sinus is rounded, not V-shaped.

There is also some doubt as to whether or not the species reported by Marcus is the same as the one considered here. His figures and description differ on numerous points.

The species was collected on algae dredged from 40-foot depths just west of Fort Macon and Beaufort Inlet, and also from drift on Bogue Banks. This species has been previously reported in the western Atlantic only from Puerto Rico (6 to 11 fathoms) and Bahia de Santos, Brazil (20 meters).

DISCUSSION

The present study includes for the most part a very limited area of the Beaufort region. As mentioned earlier, the "Beaufort region" in the literature generally includes the waters from shore to the Gulf Stream and from Cape Lookout to New River Inlet (occasionally to Cape Fear). The most intensive collections were made in the immediate vicinity of Beaufort, i.e., in the waters behind the outer banks, the material available from offshore being small by comparison.

Fifty-nine species are reported in this study. This number includes not only the species collected during the survey period but also those collected by Dr. R. C. Osburn of which specimens were available. Most of Dr. Osburn's specimens were collected from the "fishing banks" by the United States Fisheries steamer "Fish Hawk" during surveys of these reefs in the early 1900's. The species reported herein, together with previously published records, bring the total number of species known from the Beaufort region to sixty-six. In comparison, eighty-eight species are known from Woods Hole, Massachusetts, twenty-eight species from Chesapeake Bay, and over one hundred and twenty species and varieties are recorded from Brazil. About two hundred and forty-five species have been reported from Florida, the West Indies, the Gulf of Mexico, and the Caribbean Sea. With extensive future collections from the "fishing banks" the number of bryozoan species for the Beaufort region should be materially increased. These "fishing banks," which brief surveys have shown to have a typical tropical fauna, have scarcely been touched except for the study by Pearse and Williams (1951) on the reefs at New River Inlet.

Twenty species have been reported in the present work as new for Beaufort, North Carolina. Some of these are new only in the immediate vicinity while others are important as new range extensions of considerable distances. The following species which were collected in the Beaufort area are new records for the North Atlantic Ocean: *Alcyonidium hauffi* Marcus; *Chaperia galeata* (Busk); *Bugula californica* Robertson. Until the present report, *Alcyonidium hauffi* has been known only from its type locality in Brazil. This species has a peculiar sub-

strate requirement in that it has only been recorded on portions of alcyonarian stems void of polyps, a situation which holds true at Beaufort, too. The concept of *Chaperia galeata* is much confused; hence, the present designation is open to question as well as most other records of it. The new record is thus offered with hesitation until other reports can be rechecked. *Bugula californica* is well known on the Pacific coast, but has been reported in the Atlantic Ocean only from Brazil.

Records of the following species at Beaufort extend ranges southward along our east coast proper: *Barentsia laxa* Kirkpatrick; *Aeverrillia setigera* (Hincks); *Electra crustulenta* (Pallas). The closest record of *Barentsia laxa* north of Beaufort is from the Chesapeake Bay, while its nearest southern record is Brazil. The report of *Aeverrillia setigera* is intermediate between its nearest records at Long Island Sound and Puerto Rico. There is no doubt that future collections in either direction from Beaufort should reveal a continuous distribution along the coast. *Electra crustulenta* is considered a northern species. The nearest report to this vicinity is from the Chesapeake Bay; thus its southern limit is now extended to Beaufort.

The ranges are extended northward along the east coast for the following species: *Sundanella sibogae* (Harmer); *Zoobotryon verticillatum* (delle Chiaje); *Membranipora savartii* (Audouin); *Conopeum commensale* Kirkpatrick and Metzelaar; *Aplousina gigantea* Canu and Bassler; *Thalamoporella falcifera* Hincks; *Thalamoporella gothica* var. *floridana* Osburn; *Discoporella doma* (d'Orbigny); *Colletosia radiata* (Moll); *Hippoporina contracta* (Waters); *Aimulosia uvulifera* (Osburn); *Hippoporidra janthina* (Smitt); *Costazia costazii* (Audouin). Four of these species, *Sundanella sibogae*, *Conopeum commensale*, *Thalamoporella gothica* var. *floridana*, and *Hippoporina contracta*, have been reported by Pearse and Williams (1951) from the reefs at New River Inlet. Therefore the present records are new only for the immediate Beaufort vicinity, the range extensions being slight. *Zoobotryon verticillatum* has never been found attached in the Beaufort area, hence its source is presently unknown. It is possible that specimens found drifting free have been torn loose from the offshore reefs or brought in by currents from regions farther south. The nearest records are from Bermuda and Florida. *Membranipora savartii* was collected here only once, large colonies in good condition being found on a bottle washed ashore on Bogue Banks. The nearest record for the species is Florida. Whether or not this species should be considered a part of the Beaufort fauna remains to be seen, pending a thorough investigation of the offshore reefs. Dr. Osburn collected the specimens of *Aplousina gigantea* in Bogue Sound but has not reported them in the literature. The Florida Straits is the nearest locality from which it is known. The new report of *Thalamoporella falcifera* extends its range northward from the Tortugas Islands, Florida. This species is found locally on drifting gulfweed, but it is considered a part of the Beaufort fauna by the precedent set by other workers who have included the gulfweed habitat as part of their regional environment. Miocene deposits of Duplin marl at Wilmington, North Carolina, have yielded specimens of *Discoporella doma*; however, the nearest recent records of the species are from Florida. *Colletosia radiata* is a species collected by Dr. Osburn from the "fishing

banks," but unreported in the literature. Again, the closest records to the Beaufort area are from Florida. The Tortugas Islands, Florida, have previously been the northernmost record of *Aimulosia wulifera*. It was found at Beaufort off Beaufort Inlet at depths of forty feet and also on a skate egg case collected from Bogue Banks. The Gulf of Mexico and various places in the West Indies are the only known localities for *Hippoporidra janthina* on the Atlantic coast of North America. It is found in shallow waters at Beaufort and thus far only in association with hermit crabs. *Costazia costazii* has previously been known in the western Atlantic only from Puerto Rico and Brazil. At Beaufort it is a rather common component of the seaweed fauna.

Until positive identification is made, the present Beaufort record of *Proboscina* sp. will not be considered in new range extensions even though the genus is not known near here. In this same category are seven unidentified species in the writer's collection which were taken from various localities around Beaufort.

Of the twenty-four species reported by Pearse and Williams (1951) from New River Inlet, North Carolina, the following were not found and are not included in the present study, for lack of local specimens: *Crassimarginatella leucocypha* Marcus; *Caulibugula* sp.; *Cribrilina punctata* (Hassell); *Adeona violacea* (Johnston); *Hippaliosina rostrigera* (Smitt); *Hippoporidra edax* (Busk).

Tetraplaria dichotoma (Osburn) was reported by Osburn (1940) but has not been found. Though not stated by Osburn, it is presumed that his specimens came from the "fishing banks."

Shackleford and Bogue Banks form a natural dividing line between the oceanic environment and the sound-estuarine environment in the Beaufort area. In comparing the distribution of bryozoans in these areas, it was found that fifteen species (26.3 per cent) were collected only in the estuarine situations, twenty-four species (42.1 per cent) were collected only offshore from the outer banks, and eighteen species (31.6 per cent) occurred in both regions.

If the bryozoan fauna of the Beaufort region is categorized according to the north-south range distribution of its component species, it is seen that five species (8.6 per cent) are known on the Atlantic coast from Beaufort northward, twenty-seven species (46.5 per cent) reach their northern limit at or near Beaufort, and twenty-six species (44.8 per cent) range far north and south of here. If the twenty-six species which are widely distributed both north and south of Beaufort can be considered among the basic components of the bryozoan fauna of any locality along the coast from Massachusetts to Brazil, then the relative proportions of the strictly northern species and strictly southern ones within an area should be the basis for the characterization of a fauna type. Since only 8.6 per cent of the Beaufort species are northern, whereas 46.5 per cent are southern, the bryozoan fauna of Beaufort and vicinity is said to be subtropical in nature with a typical tropical fauna on the offshore reefs.

SUMMARY

1. A study has been made of the bryozoans of Beaufort, North Carolina, and vicinity, together with a survey of their local distribution and substrate preferences.

2. Fifty-nine species are reported and described herein, bringing the total number of species known from the Beaufort region to sixty-six.

3. Twenty species are new records for Beaufort. Some of these are new only in the immediate vicinity while others are important as new range extensions of considerable distances. The reports of *Alcyonidium hauffi* Marcus, *Chaperia galeata* (Busk), and *Bugula californica* Robertson are new records for the North Atlantic Ocean. The ranges of three species are extended southward along the east coast and those of thirteen species are extended northward.

4. It was found that 26.3 per cent of the species occur only in the sounds and estuaries, 42.1 per cent occur only offshore, and 31.6 per cent are distributed in both situations.

5. Only 8.6 per cent of the species are known on the Atlantic coast from Beaufort northward, whereas 46.5 per cent reach their northern limit at or near Beaufort, and 44.8 per cent range both north and south.

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A STUDY OF THE LIFE HISTORY OF THE CYPRINID FISH *NOTROPIS COCCOGENIS*

BY L. M. OUTTEN

Department of Biology, Mars Hill College, Mars Hill, North Carolina

Notropis coccogenis (Cope), the war paint shiner, is a small cyprinid fish found in the mountain streams of the upper Tennessee River system. It was described from tributaries of the Holston River, Virginia (Cope, 1867: 158, 160). Little has been published concerning this species other than with reference to nomenclature, distribution, or its association with other fishes.

From September, 1949, to June, 1955, ninety-one collections of specimens for study were made, mostly in tributaries of the French Broad River (Tennessee River system) near Mars Hill, Madison County, North Carolina. Standard length, age, sex, and maturity were determined for 1065 individuals. Studies were made of the food and the fecundity of 68 and 30 specimens respectively. Observations included feeding habits, spawning behavior, and habitat relationships. Rate of growth, time of annulus formation, maximum size, and longevity were noted.

This account was condensed from a section of a thesis submitted to the faculty of the Graduate School of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy. I wish to express my sincere appreciation to Dr. Edward C. Raney for his encouragement and many helpful suggestions in the preparation of the original part of the work. Appreciation also is expressed for the counsel of Dr. Charles E. Palm and the suggestions of Dr. Clifford O. Berg. The co-operative attitude of North Carolina Wildlife Protector Raymond C. Ramsey and associates facilitated field studies.

METHODS.—A minnow seine 8 feet long by 4 feet deep with $\frac{3}{16}$-inch mesh was used for collecting. Polaroid sunglasses were helpful in reducing surface reflections. A $2\frac{1}{4}$- by $3\frac{1}{4}$-inch press camera was used to photograph habitat, nests, eggs *in situ*, and spawning activity. The suggestions of Reighard for the study of the habits of fishes were useful (1910: 1113–1125). Preliminary collections provided information helpful in the selection of localities for further investigation.

Fairly clear, quiet water is desirable for successful observation of fish activity. At times local thundershowers stirred up sediment and greatly reduced visibility, making it necessary to seek streams with less roiled water outside the immediate area of the watershed affected. Observations concerning specimens, behavior, and habitat were recorded as suggested by Hubbs and Lagler (1947: 17–19), using field notes sheets. Nests with territory-holding or spawning fishes were observed carefully as long as activity could be seen in the area. Air and water temperatures, species over the nest, position occupied, behavior, associates, and other significant facts were noted.

SYNONYMY

Notropis coccogenis (Cope). War Paint Shiner

See original thesis (Outten, 1956: 3–7) for complete data and references.

Hypsilepis coccogenis. Cope, 1867: 158, 160 (orig. descr.); 1869: 229, 240, Pl. 23, Fig. 5 (col. fig.); 1870: 459, 493, 494 (range).

Leuciscus coccogenis [*Hypsilepis coccogenis*, Cope]. Günther, 1868, 253 (syn., descr.).

Luxilus coccogenis. Jordan, 1876: 287 (descr., range); 1877: 370 (range). Jordan and Brayton, 1878: 18, 31, 64, 85, 91–92 (descr., distr.).

Minnilus coccogenis. Jordan and Gilbert, 1883: 188 (descr., distr.).

Notropis coccogenis. Jordan, 1885: [26] (range); 1890: 142, 145, 151, 152 (descr., distr.). Gilbert, 1891: 147, 152 (loc.). Jordan and Evermann, 1896: 284, 285 (syn., descr., range); 1900: XIX, 3220, Pl. XLIX, Fig. 124 (class., fig.). Smith, 1907: 94–95 (syn., descr., distr.). Evermann, 1918: 312–315, 318, 319, 321, 324, 326, 343, 364, 366 (distr.) Hildebrand, 1932: 62–63, Fig. 1 (synon., descr., distr.). Raney, 1952: 97 (loc.)

Hydrophlox coccogenis. Jordan, 1929: 83 (descr., distr.).

Coccotis coccogenis. Jordan, Evermann, and Clark, 1930: 127 (descr., range).

Notropis brimleyi (misidentification of *N. coccogenis*). Bean, 1903: 913–914 (descr., loc.) Hildebrand, 1932: 62–64, Fig. 2 (descr., loc.).

Hydrophlox brimleyi (misidentification). Jordan, 1929: 83–84 (descr., loc.).

Coccotis brimleyi (misidentification). Jordan, Evermann, and Clark, 1930: 127 (ref. to orig. descr.).

DISTRIBUTION. *Range.*—Members of *N. coccogenis* occur in the upper Tennessee River system in Virginia, Tennessee, North Carolina, Georgia, and Alabama. The species is listed from the Big Sandy River system, Ohio River drainage, in Kentucky (Woolman, 1892: 284, 287). East of the Blue Ridge it has been found in the upper Catawba-Santee rivers drainage in Avery, Caldwell, and McDowell counties, and in South Fork New River (Ohio River system) near Boone, Watauga County, N. C. These Catawba and New systems were probably reached through stream capture or by human introduction from mountain tributaries of the Tennessee River system.

Habitat.—Small schools were observed in medium to large mountain streams having clear water and moderately rapid current. They were commonly seen over rocky, gravel, or sandy bottoms in the middle to upper levels of the larger, deeper pools. Specimens were frequently taken below and to the side of swift riffles. In such areas the velocity and volume of flow often approached the proportions of a small waterfall. At times individuals were seen headed toward the current in large pools near the center of the stream.

Local collections studied.—Observations were made on specimens of *coccogenis*

taken in tributaries of the French Broad River in Buncombe, Henderson, Madison, and Yancey counties, N. C., and in the Catawba and South Fork New river systems in the areas indicated above, under the heading, Range. These and other specimens studied are deposited in the Cornell University Fish Collection.

Associates.—Members of *coccogenis* were often accompanied by individuals of *Notropis rubricroceus* (Cope) and *Hybopsis micropogon* (Cope), especially at nests. Other associates in streams included: *Hypentelium nigricans* (LeSueur), *Moxostoma erythrurum* (Rafinesque), *Campostoma a. anomalum* (Rafinesque), *Hybopsis* sp., *H. a. amblops* (Rafinesque), *Notropis galacturus* (Cope), *N. leuciodus* (Cope), *N. spectrunculus* (Cope), *N. spilopterus* (Cope), *Phenacobius uranops* Cope, *Rhinichthys atratulus obtusus* Agassiz, *Etheostoma flabellare* Rafinesque, *E. swannanoa* Jordan and Evermann, *Percina evides* (Jordan and Copeland), *Micropterus d. dolomieui* Lacépède, *M. salmoides* (Lacépède), and *Cottus bairdi* subsp.

Predators.—Members of *M. d. dolomieui* and *M. salmoides* gave evidence of preying upon individuals of *coccogenis*. The common water snake, *Natrix s. sipedon* Linnaeus, and the belted kingfisher, *Megaceryle a. alcyon* (Linnaeus), were seen in the vicinity of streams inhabited by the species studied.

GENERAL BEHAVIOR.—Singly, or in small groups, individuals head upstream in the larger pools and characteristically move rapidly from one area to another. They are active during daylight throughout the year.

REPRODUCTION. *Age and size at maturity.*—Age and growth studies indicate that most individuals of *coccogenis* attain maturity when two years old. Among the age-group II specimens from the Ivy Creek system the males ranged in standard length from 70 to 89 mm., with a mean of 77.0; the females from 59 to 83 mm., with a mean of 74.8.

Sexual dimorphism.—The males of *coccogenis* are generally larger than the females, as shown above. The average standard length of the males was equal to or greater than that of the females in 10 to 14 collections of the age-group II specimens studied or 77.8 per cent of the times when both were present. The pectoral and pelvic fins of the male are slightly longer than those of the female.

A male taken in Little Ivy Creek on July 1, 1954, preserved, and examined shortly after reaching the laboratory, appeared somewhat greenish dorsally and was silvery along the lower sides of the body. In the stream, the upper part of the body is light greenish tan to mildly olivaceous. There is a reddish-orange vertical line on the anterior part of each opercle. At spawning time the males of *coccogenis* showed pronounced reddish coloration on the snout and sides of the body; the females appeared much paler.

In early June, near the time of observed spawning activity, the male had two to three irregular rows of single-pointed, moderately large tubercles extending from the angle of the jaw along the edge of the mouth to the tip of the chin. From the anterior part of the snout the tubercles extended posteriorly on either side in two similar rows, became three rows below the nostrils, spread out slightly in front of the eye, continued dorsad as one row, and ended directly above the eye. The rays of the pectoral fins had many well-developed tubercles on the dor-

sal surface, but few were present ventrally. The rays of the pelvic fins had moderate pearl organs dorsally and except along the leading edge of the first were smooth ventrally. Tubercles on the dorsal fin rays were small and more numerous distally. Likewise, those on the rays of the anal fins were poorly developed and more abundant distally but slightly larger anteriorly. Pearl organs on the caudal fins were very small and mostly toward the ends of the rays. There were no tubercles on the scales.

The tubercles of females taken in early June were small and poorly developed. Often they barely emerged from the surface and on some specimens appeared as a group of four to five faint prominences in front of the eye and below the nostril, then extended in a single line along the lower margin of the snout with additional ones on the lower jaw. The external surface of other parts of the body, including the fins and scales, was smooth. The scales of breeding males had a considerably thickened, glistening, epidermal coating, which was not developed to such a noticeable extent on the females. The side of the body of the male is fairly straight; that of the female, especially when swollen with eggs, tends to be slightly rounded.

Fecundity.—A study was made of the ovaries and eggs of thirty preserved specimens of the larger swollen females, ranging from 60 to 106 mm. in standard length, one to four years in age, and collected from April 3 to June 13 in tributaries of the French Broad-Tennessee rivers system.

Ovaries.—The ovaries of mature females are elongate, broad, deep, and somewhat V-shaped in cross-section. They extend from the transverse septum to the posterior part of the abdominal cavity and occupy much of the space ventral to the air bladder, just above the alimentary canal. Developing eggs tend to give the surface of the ovaries a granular appearance. The paired ovaries were removed intact, so far as their condition would permit, placed in a watch glass, and studied with the aid of a binocular dissecting microscope. Measurements of the length, width, and depth of the ovaries showed that the dimensions of the organs were in direct relation to the maturity and size of the individual, number of mature eggs present, and proximity of the spawning season.

Testes.—The testes are thin, narrow, and threadlike in immature specimens; slender and cordlike in developing individuals; much enlarged, rounded, and milky white in mature males during the period preceding the spawning season.

Eggs.—The spherical eggs consist largely of pale yellow yolk. Mature eggs preserved in formalin measured about 1.5 mm. in diameter. Those less than 1 mm. in diameter did not appear likely to be spawned soon and were considered immature. Using a Magni-Focuser with a magnification of about 3×, actual counts were made of all visible eggs in both ovaries. The eggs were counted in two groups—those that approached maturity and measured from 1 to 1.5 mm. in diameter and immature ones less than 1 mm. in diameter. The number of eggs of each size was recorded for the ovaries studied.

Although most of the females collected in early April had many eggs less than 1 mm. in diameter, there was a considerable number of larger eggs in some of the individuals. Ovaries of specimens taken from late April to about the middle

of June contained a greater proportion of larger eggs, about 300 to 750 of mature size. A maximum number of 1636 mature eggs was found in a four-year-old, 106-mm. specimen taken on June 5. All eggs of the one-year-old specimens studied, in addition to those of some of the two-year-old and older females, were less than 1 mm. in diameter, indicating that members of *coccogenis* do not generally attain maturity when one year old. Age-and-growth studies showed that some of the more mature, apparently early-spawned individuals have slightly enlarged eggs and gonads during the late spring and summer of their second year.

Spawning habits. Spawning site.—A collection of small fishes, including some fine specimens of *coccogenis*, was taken on September 15, 1953, in Big Laurel Creek (Laurel River) near Hurricane junction, a short distance upstream from the mouth of Little Hurricane Creek and the bridge at the intersection of highways U. S. 25 and 70, and N. C. 208. During the following spring spawning was observed here.

Hurricane junction is 6 miles east-northeast from Hot Springs, 11 miles north-northwest from Marshall, and 22.3 miles northwest from Mars Hill, N. C. Big Laurel Creek joins the French Broad River about 3½ miles south-southwest from Hurricane junction. The stream in this area is about 1595 feet above sea level.

Habitat.—Big Laurel Creek is about 90 feet wide in the area of the studies. The stream ranged from about 6 inches deep in the rapids to 3 or 4 feet deep in a slightly impounded area about 0.3 mile upstream. The bottom consisted of coarse, rocky rubble with gravel and sand in the quieter areas. Submerged rocks in the shallow water of the riffles were covered to a considerable extent with riverweed, *Podostemum ceratophyllum*. Other rocks seemed to be relatively bare save for a thin film of algae on some. The water was white and fairly clear except immediately after rains. The current was moderately fast in the rapids, barely perceptible in the quiet area upstream.

Nest.—Members of *coccogenis* spawned over a nest of the river chub, *Hybopsis micropogon*. The nest was 3½ feet long by 2 feet wide. It consisted of a pile of small stones and coarse gravel ½ to 1½ inches in diameter. Located in water 7 to 13 inches deep, it was about 3½ feet from the bank and partly enclosed on three sides by moderately large rocks. There was a small pool about 20 inches deep at each end of the nest, upstream and downstream.

The tendency of some cyprinids to utilize the nests of other fishes, as *H. micropogon*, has been noted by Greeley (1929: 172), Hankinson (1920: 8; 1932: 415–417, 423), Hubbs and Cooper (1936: 45), Raney (1940a: 6; 1940b: 128; 1940c: 363; 1947: 125; 1950: 161), and Reighard (1943: 416–423).

Pre-spawning activities.—During the period of June 8 to July 17 from 9:20 a.m. to 5:30 p.m. when the temperature of the air was 72° to 83.5° and the water 67.5° to 81.5° F., small groups of eight to ten or fewer brightly colored males of *coccogenis* were observed as they held territories over nests of *H. micropogon*. The largest male took the foremost position, about an inch above the small stones. Sometimes as they contended for positions over the nest, he drove the

others away from his location and continued to dominate the area. When the challenger was about the same size as the defender the two males swam off to the side for a short distance. Scattered over the entire stream side of the nest, members of the group maintained fairly constant positions as they swam slowly toward the current. Continually moving, they made short, quick darts at would-be intruders and kept other fish away from the area.

Spawning.—On June 11 and 12 at various times from 9:45 a.m. to about 5:00 p.m. with temperatures of the air from 76° to 81.5° and the water 68° to 75° F. aggregations of *coccogenis* were seen spawning over a nest of *H. micropogon*. The entire group was headed toward the current with the males in the upstream positions; the females were to the rear and slightly above them. In spawning, a female moved forward to a position near a male. The two remained side by side for a brief moment, then together they settled down in a crevice between the stones on the bottom of the upstream part of the nest. With considerable vibration of their bodies eggs and sperm were discharged. Other males of *coccogenis* crowded around the pair.

The territory-holding and challenging behavior of males of *coccogenis* and the manner in which, preparatory to egg laying, a female moved forward to a position near that of a male resembled the spawning activities of *Notropis cornutus*, which have been described by Raney (1940a: 5–11).

Associates.—From time to time a moderate-sized male of *H. micropogon* brought small stones to the nest over which individuals of *coccogenis* were active. Members of *Notropis rubricroceus* held territories and for a short period spawned over another part of the same nest as that used by the aggregation of *coccogenis*. The spawning activity attracted other fish to the area, especially immature individuals of *H. micropogon*. They rushed in and each pushed around among the stones with his snout in what seemed to be efforts to get the recently deposited eggs. A largemouth bass, *Micropterus salmoides*, occupied an adjoining pool and made quick, feeding thrusts, causing the spawning group to disband from time to time. The disturbance was continued until finally none of the individuals returned to the area.

Post-spawning observations.—No activity was seen over the nest during the days immediately following the observed spawning. About ten days later, June 21, a male of *coccogenis* was found swimming feebly at the surface near the middle of the stream. A more active similar male was seen the same morning as it swam over the nest area. Individuals and small groups of the species were seen in other streams on June 30 as well as July 1 and 17.

AGE AND GROWTH. *Specimens studied.*—In the age-and-growth study, 1065 specimens of *coccogenis* from 62 collections were used. Of these, 204 were taken from Little Ivy and Bull creeks, 147 from other streams of the French Broad River system near Mars Hill, and others from Cane and Johns rivers, N. C. The dates of the collections ranged from January 17 to November 7 during 1950 to 1955. Additional specimens were obtained from the Cornell University Fish Collection.

Methods.—The standard length in millimeters was determined by measuring

with dividers the distance from the tip of the snout to the end of the hypural plate as described by Hubbs and Lagler (1947: 13–14). The sex of each specimen was ascertained by examination of the gonads through a longitudinal slit made along the midventral line from the vent to the region between the pectoral fins. A binocular dissecting microscope was used to study the internal anatomy.

Scales of the specimens were examined in the manner described by Creaser (1926: 3) and Raney and Lachner (1943: 229). Age of the specimens was determined by the scale method, the validity of which has been demonstrated for other species by Hile (1941: 201–205), Van Oosten (1923: 410), and others (see literature cited).

A few scales were taken from the right side in the area below the origin of the dorsal fin and above the lateral line. Sometimes much of the squamation in the region consisted of replacement scales, which made necessary the removal of a larger sample in order to get readable material. The scales were placed in a drop of water on a glass slide, cleaned gently with a smooth-surfaced, blunt instrument, transferred to a clean drop of water on another part of the slide, and studied with the aid of dissecting and compound (50×) microscopes.

During the early part of the study various mounting media including Canada balsam, Permount, glycerine jelly, and polyvinyl alcohol were tried for the scales. Not any of these was found to meet completely all requirements. Some scales covered with cellophane tape as a temporary mountant were found to be in good condition after a period of two years. Water preparations proved to be satisfactory and were used for routine studies.

Permanent mounts were made of a series of typical scales in order to compare the development at different seasons of the year. Staining the cleaned scale lightly with a two per cent potassium hydroxide solution of alizarine red S, in a manner similar to that described for skeletal structures by Evans (1948: 44), produced a more distinct outline of the scale features. The scales were dehydrated gradually in a series of solutions of alcohol with concentrations increasing from 40 to 99 per cent, cleared in beechwood creosote for two minutes, mounted in euparal (as used in the studies of Lagler, 1936: 4–5), and covered on a glass slide.

Description of scales.—The terms used for scale structures are according to the descriptions of Creaser (1926: 63–65) and Lagler (1947: 150–151). The scales of *coccogenis* are broadly oval, with the width one and one-half times the length and the outer surface smooth. The margin is slightly rounded anteriorly, widely V-shaped to broadly rounded posteriorly, and almost straight along the short lateral areas. The sides taper anteriorly slightly so that the widest part of a scale is in the posterolateral region. The focus is located about halfway between the center of the scale and the anterior margin. Generally there were about 6 primary and 7–11 or more secondary apical radii, which made a total of 13–17 or possibly 20 as described by Cockerell and Calloway (1910: 190–191, 195). The circuli were broadly circular, concentric, and fairly regular. The distinct annulus was shown by the cutting over of circuli in the posterolateral fields, wider spaced ridges in the area corresponding to the early part of the growing season, and closer spacing toward the end of the period.

Age determination.—Counting the number of annuli has been shown by many workers, as indicated above, to be a valid method for ascertaining the age of fish. The present study indicates that this is a reliable means for determining the age of specimens of *coccogenis*, the younger members especially. Scales of individuals three years of age or older often show greater irregularities near the outer edge.

Time of annulus formation.—Stream temperatures taken during the middle to late afternoon in Little Ivy Creek near Mars Hill, N. C., were about 62° in early April, 64° to 75° in late April to early May, and 66° to 77° F. in late May. Beckman (1943: 303), Raney and Lachner (1943: 230–232; 1946: 79–81, 85), and others have observed for different species that annulus formation is associated with temperature increase in the surroundings.

Specimens of *coccogenis* collected near Mars Hill on April 3 and 10 had no circuli beyond the outermost annulus. Most of those collected on April 25 (25 specimens) likewise had no circuli beyond the outer annulus, while three had one ridge beyond this structure. All collected on May 2 had one circulus beyond the outer annulus. Specimens collected on May 25 and 26 averaged two to three circuli beyond the outer annulus. Conditions near Mars Hill, N. C., were such that generally most individuals of *coccogenis* seemed to form the annulus about the last week in April.

Rate of growth.—During the period from July 3 to September and October the increase in standard length for young-of-the-year males was 23.4 mm. (89.3 per cent), females 21.3 mm. (81 per cent) (Tables I and II). One-year-old specimens taken from Little Ivy and Bull creeks during the period from September 15 to October 18 showed increases in standard length of 23.4 mm. (41.6 per cent) for males and 16.2 mm. (30.4 per cent) for females over those taken between April 3 and July 3. The average increase in standard length of age-group II individuals from spring to fall was 15 mm. (21 per cent) for the males and 4.1 mm. (5.6 per cent) for the females. Three-year-old specimens taken during the period from April 3 to July 3 showed an increase for the males of 3 mm. (3.5 per cent) and for the females 3.5 mm. (4.5 per cent) over those of age-group II collected in the fall. There was a general pattern of rapid growth during the first two years with additional but much smaller increments the following years, as shown in Tables I–III.

Maximum size.—The largest specimens were each 106 mm. in standard length and four years old, a female taken in Little Ivy Creek near Mars Hill, N. C., April 25, 1953, and a male obtained from a tributary of Laurel Creek near the Tennessee-North Carolina state line June 5, 1952.

Longevity.—Of the specimens studied, 315 (29.6 per cent) were of age-group O, 584 (54.8 per cent) age-group I, 136 (12.8 per cent) age-group II, 25 (2.3 per cent) age-group III, and 5 (0.5 per cent) age-group IV. There was a sharp decrease in the number of individuals living beyond the second summer. Age-group II represented a decrease of 78.1 per cent of the preceding age group, while age-group III was 81.6 per cent less than the next younger year class. The small number of four-year-old specimens remaining showed a decrease of 80 per cent of the preceding age group.

Among the young of the year and the age-group-I specimens there was little difference in the number of males and females present. Those two and three years of age included a greater number of females, 66.2 and 76 per cent respectively, somewhat as found by Pfeiffer for three-year-old *Notropis rubellus* (1955: 101). However, the presence in age-group IV of a slightly greater number of males tends to reverse the apparent trend of the younger groups. The five specimens that were four years old, three males and two females, were taken during the period from April 4 to June 7. No individuals of five years or greater age were observed.

TABLE I

Length-frequency distribution according to age and sex of 204 specimens of Notropis coccogenis *collected in Little Ivy and Bull creeks, Madison Co., N. C.*

Date	April 3–July 3									Sept. 15–Oct. 18					
Age Group	0		I		II		III		IV	0		I		II	
S.L. (mm.)	M	F	M	F	M	F	M	F	M	M	F	M	F	M	F
106									1						
103															
100															
97															
94							1								
91							1								
88							1							1	
85							1					2		1	
82												3			1
79						1		1				1			—
76					1	7						1			3
73					—	4						—	3		
70			1		3	1						—	—		
67			1			1						—	2		
64			2	1		—						—	1		
61			3	4		1						2			
58			5	12						2					
55			6	3						4	1				
52			14	2						6	8				
49			8	6						4	5				
46			3	6						6	9				
43			2	3						3	4				
40										1	2				
37															
34															
31	1														
28	5	5													
25	4	3													
22	2	1													
No. of specimens...	12	9	45	37	4	15	4	1	1	26	29	9	6	2	4
Mean.....	26.2	26.3	53.6	53.3	71.5	73.4	89.5	81	106	49.6	47.6	77.0	69.5	86.5	77.5

TABLE II

Standard-length distributions (in mm.) by age and sex of Notropis coccogenis *from the Ivy Creek system near Mars Hill, Madison Co., N. C.*

Range, mean, and number of specimens (in parentheses) are given

Locality	Date	Age Group								
		0		I		II		III		IV
		M	F	M	F	M	F	M	F	M
Bull Creek	July 3	23–31 27.2 (12)	22–30 27.3 (9)							
Little Ivy Creek	Sept. 15–16	40–49 45.0 (4)	41–45 42.7 (3)	78–86 82.8 (7)	65–75 70.8 (6)					
	Sept. 20	43–57 48.8 (6)	43–54 48.0 (6)	62 62 (2)			83			
	Oct. 18	46–60 52.8 (16)	45–55 49.7 (20)			85–89 87 (2)	76–77 76.7 (3)			
	April 25			48–59 54.0 (16)	45–56 50.3 (7)	70–76 73.0 (2)	61–77 69.0 (2)			106
	May 25–26			52–68 56.9 (7)	49–60 56.8 (4)		69–77 75.1 (7)	91–96 93.5 (2)	81	
	May 31			45–53 49.4 (13)	45–60 49.3 (10)					
McKinney Branch	June 13			33–45 38.8 (5)	35–47 40.6 (14)					

Effects of environment.—Temperature increases during the spring were accompanied by body growth and annulus formation as shown for other species by Cooper (1936: 587, 589) and others. Heavy rains over the watershed caused greatly increased volume of flow in streams. The sedimentation that followed was hazardous to eggs and young as well as injurious to adults. Local, seasonal, and annual differences in climatic and other environmental conditions seemed to influence variations in development.

FOOD AND FEEDING. *Specimens studied.*—From collections made during the spring, summer, and fall seasons, 68 of the larger, adult specimens were selected

for food studies. The periods represented by the specimens were as follows: spring, March 24 to April 25; summer, June 13 to August 31; and fall, September 20 to November 7. Larger individuals, 37 males and 31 females, were selected at random for study. The specimens used ranged from 58 to 101 mm. in standard length and from one to four years old.

TABLE III

Standard-length distributions (in mm.) by age and sex of Notropis coccogenis *from the French Broad River system, other than Ivy Creek and tributaries*

Range, mean and number of specimens (in parentheses) are given

Locality	Date	Age Group									
		0		I		II		III		IV	
		M	F	M	F	M	F	M	F	M	F
Webb Creek, Sevier Co., Tenn.	July 24	25–32 28.1 (8)	27–29 28.0 (4)	47–58 58.1 (5)	38–56 45.9 (10)	79	68		82–91 86.3 (3)		
Trib. French Broad R., Sevier Co., Tenn.	Aug. 31	31–53 40.9 (24)	36–49 40.9 (16)	61–84 73.0 (7)	55–76 64.8 (20)		76		79		
Big Laurel Creek, Madison Co., N. C.	Sept. 12	30–52 40.2 (22)	31–45 38.3 (23)	60–82 73.4 (5)	55–66 60.5 (2)		76–88 78.0 (3)				
Spring Creek, Madison Co., N. C.	Sept. 12	42–59 51.3 (14)	40–48 45.0 (12)	86	74–78 76.7 (3)						
French Broad River, Buncombe Co., N. C.	April 4			37–52 43.1 (7)	39–48 43.5 (6)		67–73 70.0 (2)	87	73		
Trib. French Broad R., Henderson Co., N. C.	April 4			31–49 42.0 (15)	28–46 41.4 (11)	50–75 61.5 (18)	53–69 60.5 (15)		77–84 80.5 (2)	92–101 96.5 (2)	
French Broad R., Cane Creek, Henderson Co., N. C.	April 8			21–46 32.2 (6)	31–34 32.0 (5)	66–84 75.0 (5)	56–63 60.5 (6)		73–80 76.5 (2)		
Spring Creek, Madison Co., N. C.	April 10			38–50 42.8 (4)	36–47 40.6 (17)						
Dry Creek, Unicoi Co., Tenn.	April 25			23–48 31.5 (13)	24–32 29.2 (10)	54	54				
Trib. Swannanoa R., Buncombe Co., N. C.	June 7			30–47 42.5 (8)	28–46 40.9 (14)	80		98			96

Method of analysis.—The procedure followed in the study was like that used by Raney and Webster for *Ameiurus n. nebulosus* (1940: 206). The standard length, age, and sex of each specimen studied were determined and recorded.

Structure of the alimentary tract.—At the posterior end of the esophagus and in line with the transverse septum is a pronounced constriction, the cardiac sphincter valve. The short bile duct extends from the right lobe of the liver and joins the adjacent part of the alimentary tract at a point about 4 to 4.5 mm. posterior to the cardiac valve in large specimens. No pyloric valve or ceca were observed. Beyond the esophagus, the relatively short alimentary canal includes that part of the digestive tract from the cardiac valve posteriorly to the region of the first bend (the stomach area or "stomach"), then turns to the left, extends cephalad to the anterior part of the abdominal cavity, has another flexure, and continues caudad in a straight line to the anal opening. Being without any pronounced enlargement in the stomach area and lacking gastric glands, the Cyprinidae are described as not having a true stomach; see Ihle, van Kampen, Nierstrasz, und Versluys (1927: 561) and Wiedersheim and Parker (1897: 257). The stomach area of each specimen used in this part of the study was removed, placed in a watch glass, and its contents examined with the aid of a dissecting microscope.

Materials taken as food.—The stomach contents were separated into groups of similar organisms corresponding to the major phyla, with members of class Insecta arranged according to orders. More specific identification was made as the condition of the material permitted. The frequency and percentage content of the food items in each stomach were recorded, indicating the animal, vegetal, aquatic, or terrestrial nature of the material. Separate studies were made for each of the three seasons. The data were summarized for each season, giving the percentage of stomachs containing the food and the percentage content of the item by volume. A summary was also prepared for the entire period from March 24 through November 7 showing for each food item the number and percentage of stomachs in which it was contained, the total volume content percentage, and the number and average per stomach (Table IV).

Ephemerida ranked first in total number of stomachs with food, percentage content, number of food organisms eaten, and average per stomach. Mayfly nymphs were the most common form of food in the spring. Terrestrial Hymenoptera, numerous in the food of specimens collected in the summer, consisted of adult ants, bees, wasps, and a sawfly. The Coleoptera taken as food were all terrestrial adults. Diptera in the stomach contents of specimens taken during the spring and summer were primarily terrestrial adults, while those of the fall were mostly immature aquatic forms. The Hemiptera eaten included adult and nymph lace-bugs (Tingidae), white fly nymphs (Aleyrodidae), and a small water boatman (Corixidae). There was a lacewing fly, order Neuroptera, in the food of a specimen taken in the fall. Lepidoptera pupae were found in the stomach contents of some of the summer and autumn specimens, as were chitinized parts of insect exoskeletons resistant to digestion. Three oligochaete worms, one aquatic and two terrestrial (*Lumbricus*), were each in the stomach contents of different specimens from the spring collections. Adult spiders, although found in the food of each season, were more abundant in the stomach contents of specimens taken

in the fall. A moderately large centipede was among the food items of a specimen from the spring season. Vegetal matter in the stomach contents included a small amount of the alga *Batrachospermum*, some bark from the spring-, and seed from the summer- and fall-season specimens.

Feeding habits.—The diet consists largely of animal matter, primarily insects. Aquatic and terrestrial forms were found in varying but not significantly different amounts, indicating that to a considerable extent food may be taken in accord-

TABLE IV

Food of 44 specimens of Notropis coccogenis *collected from March 24 to Nov. 7*

Of 68 stomachs examined, 44 had food. Specimens were 58 to 101 mm. in standard length, one to four years old. Under each season the left column represents the percentage of stomachs with food, the right the percentage content of food by volume.

	Spring March 24–April 25		Summer June 13–Aug. 31		Fall Sept. 20–Nov. 7		Total for three seasons				
							Stomachs with food		Vol. %	No. of organisms	
Stomachs, examined	23		30		15		No.	%		Total	Av. per stomach
with food	21		12		12						
Food Item											
Aquatic Organisms	90.0	58.9	33.3	9.8	63.6	28.2	30	68.2	32.3	54	1.8
Terrestrial Organisms	47.6	41.1	91.7	90.2	90.9	71.7	31	70.5	67.7	136	4.4
Animals	100.0	98.1	100.0	99.7	90.9	88.0	43	97.7	95.2	177	4.1
Vegetation	4.9	1.9	8.3	0.3	45.5	12.0	7	15.9	4.7	13	1.9
Insecta	100.0	94.5	100.0	98.8	72.7	69.1	41	93.2	87.5	168	4.1
Ephemerida	76.2	44.9			36.4	10.7	20	45.5	18.5	120	6.0
Hymenoptera	28.6	3.7	58.3	52.5	45.5	14.3	18	40.9	23.5	28	1.6
Coleoptera	47.6	27.3	25.0	19.2	18.2	7.3	15	34.1	17.9	38	2.5
Diptera	23.8	4.1	25.0	9.7	36.4	14.6	12	27.3	9.5	38	3.2
Trichoptera	19.0	7.4	8.3	8.3	18.2	2.0	7	15.9	5.9	7	1.0
Hemiptera	4.8	0.5	16.7	0.6	36.4	8.8	7	15.9	3.3	12	1.7
Plecoptera	23.8	5.5	8.3	0.8	9.1	0.9	7	15.9	2.4	8	1.1
Lepidoptera			8.3	7.8	9.1	9.1	2	4.5	5.6	2	1.0
Odonata	4.8	0.5			9.1	0.5	2	4.5	0.3	2	1.0
Neuroptera					9.1	0.9	1	2.3	0.3	1	1.0
Insect remains	9.5	0.6					2	4.5	0.2	2	
Arachnoidea	4.8	0.7	8.3	0.8	27.3	18.9	5	11.4	6.8	5	1.0
Oligochaeta	14.3	1.7					3	6.8	0.6	3	1.0
Chilopoda	4.8	1.2					1	2.3	0.4	1	1.0
Vegetation	4.8	1.9	8.3	0.3	45.5	12.0	7	15.9	4.7	(13 lots)	
Vascular plants					45.5	11.9	7	15.9	4.67	(12)	
Algae					9.1	0.1	1	2.3	0.03	(1)	

ance with its abundance. Much of the food was obtained in the current or at the surface of moderately rapid mountain streams. While headed toward the current in a fairly stationary or slowly moving position, feeding individuals were seen to open their mouths slightly at frequent intervals as food was taken. At times they would rise rapidly to the top of the stream to grab objects that fell on the surface of the water.

Factors influencing food eaten.—The large, protrusible, obliquely terminal mouth is suited to taking food in the stream or at the surface, as described for other species by Evans (1950: 18, 85). The sharp-pointed, raptorial pharyngeal teeth with narrow grinding surfaces are associated with carnivorous feeding habits. The simple digestive tract without ceca is better suited to a concentrated diet of animal food. The presence of food in only twelve stomachs of thirty specimens collected during the period of spawning activity suggests that there was reduced feeding at that time.

SUMMARY

Members of *coccogenis* occur in the upper Tennessee River system in Virginia, Tennessee, North Carolina, Georgia, and Alabama. They have also been found in the headwaters of the New and Catawba rivers drainages in North Carolina.

Individuals and small groups headed upstream in the larger pools of medium-sized mountain streams, especially those below and to the side of swift riffles. Activity was observed during the daytime throughout most of the year. Associates were forms commonly found at moderate elevations in southern mountain streams west of the Blue Ridge. *Micropterus d. dolomieui* and *M. salmoides* were predators of this species.

During the spawning season, males showed pronounced reddish coloration on the snout and upper parts of the body; the females were paler. At the same time the tubercles of the males were moderately large on the snout, lower jaw, and dorsal surface of the pectoral fin rays. The poorly developed tubercles of females were limited to the chin and snout.

Mature eggs of preserved specimens measured about 1.5 mm. in diameter. There was a pronounced increase in the number of mature eggs and the size of the ovaries during the period immediately preceding spawning.

At times from June 8 to July 17 males of *coccogenis* held territories over the upstream part of nests of gravel arranged in a pile by males of *H. micropogon*. Spawning was observed on June 11 and 12 when the water temperature was from 68° to 75° F. A female moved forward from the downstream edge of the nest to a position near that of a territory-holding male. After a short pause they settled down together to the bottom where with much vibration of their bodies spawning took place.

The broadly oval scales are cycloid with the posterior margin roundly V-shaped. They have concentric circuli and 13–17 apical radii. Scales selected from 1065 preserved specimens indicated that near Mars Hill, N. C., generally most individuals of *coccogenis* formed the annulus about the last week in April.

Some members of each sex seemed to approach being fully developed during

the second summer; most became mature as two-year-olds. Greatest increase in size occurred during the early growing period with smaller increments thereafter. The average size of the males was generally equal to or greater than that of the females. The maximum size of 106 mm. in standard length was attained by a male and a female, each four years old. This was also the age of the oldest individuals. Males and females were about equal in number. The life span was relatively short.

The food was largely insects. Ephemerida ranked first among the orders taken. Aquatic organisms made up most of the spring nourishment. Terrestrial forms were more abundant in the stomach contents of specimens taken during the summer and fall periods. Feeding took place in the upper depths and at the surface of streams.

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AN ANNOTATED LIST OF NORTH CAROLINA EARTHQUAKES

BY GERALD R. MACCARTHY

Department of Geology and Geography, University of North Carolina, Chapel Hill, North Carolina

Although North Carolina is not usually considered to be a particularly seismic state, a considerable number of earthquakes have occurred within its borders, three of which are listed by the United States Coast and Geodetic Survey as "important". These three are: February 21, 1916, felt over 200,000 square miles; October 20, 1924, felt over 56,000 square miles; and November 2, 1928, felt over 40,000 square miles. Many others, whose epicenters were elsewhere, were also felt in this state. When a seismological station was established at the University of North Carolina in 1953 it became desirable to make a study of the true seismicity of the state: this paper is an attempt to list, insofar as possible, all quakes which have been felt in North Carolina whether or not they originated within the state. Doubtless many have been missed, especially during colonial times,

and the author would appreciate it greatly if anyone knowing of a quake which has been missed would send him such data as may be available concerning it.

Special attention has been paid to those minor and lesser known shocks which have received little attention in the literature; those about which much has been written elsewhere do not receive mention commensurate with their importance.

In individual accounts most references to major sources of information are abbreviated; a complete listing of such sources is given at the end of the paper. Times are given in the 24-hour system; e.g., 2:30 p.m. is written as 1430 hrs. When known, times are given to the nearest minute and in some few cases to the nearest second. No attempt has been made to distinguish between "local" and "eastern standard" time although in general the earlier events (those before 1883) are recorded in the local, and the later events in the standard system. Where earthquake intensities are given without further qualification, they are those assigned by the United States Coast and Geodetic Survey which, in its *Earthquake History of the United States*, uses the Rossi-Forel scale with a range of from 1 to 10. Material added by the writer has been inclosed in square brackets wherever necessary to avoid confusion. Starred items are quakes whose epicenters appear to have been in North Carolina or on its borders.

*1774: February or March 21, about 1500 hrs. Felt in the Winston-Salem area. "On March 21, in bright sunshine, there was an earthquake which lasted about one minute, but did no harm." (Mor. Recs. 2, p. 816; Salem Diary.) "February 21st: Today at three o'clock there was an earthquake. The bells hanging in the store all rang at the same time; I was in the yard and thought a large herd of cattle was coming. It was felt in all the houses, but not severely enough for all to notice it." (Mor. Recs. 2, p. 832; Bethabara [Oldtown] Diary.) Despite the disagreement in date, both these references doubtless refer to the same earthquake.

*1776: Night of November 5–6. Jackson County. "That night we lay upon a prodigious Mountain where we had a Severe Shock of an Earthquake, which surprized our men very much." (Report of Captain William Moore to General Rutherford of his Command during the Expedition against the Cherokees. *In* Col. Recs. X, p. 897.) According to Berlen C. Moneymaker, Chief Geologist, T.V.A., who called my attention to this, the "Prodigious Mountain" is in Jackson County, between the Tuckasegee River and Richland Creek, which latter is a tributary to the Pigeon River. Moneymaker estimates the intensity as 4 to 5 on the Wood-Neuman scale.

*1787: November 9 and 10. Felt in the Winston-Salem area. "November 9. During the Friday liturgy [Nov. 9] and during the night of the 10th, various Brethren noticed a slight trembling, and as no cause could be found, it was concluded that it was a slight earthquake." (Mor. Recs. 5, p. 2174; Salem Diary.)

*1792: August 11, between 2100 and 2200 hrs. Felt in the Winston-Salem area. "In the evening between nine and ten o'clock several Brethren who were on the streets heard a rumbling under the earth, felt a slight quiver, and at the same time saw a ball of fire above our town. The same thing was seen at Friedberg,

Friedland, and Bethabara, and the rumbling noise was also heard in those places." (Mor. Recs. 5, p. 2363, Salem Diary.) This was probably the shock-wave of a large fireball meteor rather than a true earthquake: compare the April 21, 1955, occurrence.

1811: November 27, about 0300 hrs. Felt in the Winston-Salem area. "Nov. 27: This morning at three o'clock, we felt an earthquake, which was particularly noticeable in the country around us. No damage was done." (Mor. Recs. 7, p. 3138, Salem Diary.)

1811: December 6, about 0200 hrs. The first main shock of the great New Madrid, Mo., series of earthquakes, which were generally felt throughout the southeastern states. "Epicenter at about 36.6° N., 89.6° W. Intensity 10. Felt over 2,000,000 square miles. A second shock, early in the morning, fully as severe as the first." (E. Hist.) Mentioned in the *Raleigh Register* for Jan. 31, 1812, and in the *Raleigh Star* for Dec. 20, 1811 and Jan. 3, 1812. The *London Times* for Jan. 28, 1812, carries a news story about this quake headed, "Earthquake in North Carolina". Communications being what they were in those days, this earthquake was quite generally ascribed to western North Carolina—Buncombe County in particular—for several weeks after its occurrence. It received the following mention in the *Moravian Records:* "December 16: In the third hour of the morning there was a fairly strong earthquake shock, which was repeated in the eighth hour, but much less severely." (Mor. Recs. 7, p. 3139; Salem Diary.) "December 16: between two and three o'clock this morning an earthquake was felt in our town and neighborhood. Many of our members were awakened, and in the church and parsonage the doors rattled suddenly and waked us." (Mor. Recs. 7, p. 3156; Bethabara Diary.) "December 15 (*sic*): In the third hour of the morning we felt an earthquake, and in the eighth hour another, although less severe." (Mor. Recs. 7, p. 3160.)

1812: January 23, early morning. Second of the main shocks of the New Madrid series. Generally felt throughout North Carolina. "The earthquake which was felt in this city [Raleigh] on Thursday week, was likewise felt in many other parts of the state. . . . In several towns from which we have heard, the shock was as violent as that which occurred in December." (*Raleigh Register*, Jan. 31, 1812.) "An earthquake was felt strongly in Mecklenburg County about 9 o'clock on the morning of January 23. . . . Another shock was felt in this city [Raleigh] about 4 o'clock on Friday morning last [Feb. 7]." (*Raleigh Register*, Feb. 14, 1812.) "A shock of an earthquake was felt by many of the inhabitants of this city [Raleigh] between 8 and 9 o'clock yesterday morning—its duration was about one minute." (*Raleigh Star*, Jan. 24, 1812.) "The earthquake of the 23rd inst. has been generally observed, and is said to have been much more severe than any of those which happened in December." (*Raleigh Star*, Jan. 31, 1812.) "Jan. 23: This morning about nine o'clock we again felt an earthquake." (Mor. Recs. 7, p. 3165; Salem Diary.)

1812: February 7, early morning. Third and last of the main shocks of the New Madrid series. Generally felt throughout North Carolina. "We have received from a correspondent in Mecklenburg a long account of the earthquake

felt in that county on the 7th ult." (*Raleigh Register*, Mar. 6, 1812.) "Another shock was felt in this city [Raleigh] and various other places, about 4 o'clock on Friday morning last" (*Raleigh Register*, Feb. 14, 1812.) "On February 7 an earthquake shock was reported from New Bern, North Carolina, and two weeks later there was a heavier shock in Mecklenburg County." (Mor. Recs. 7, p. 3162.) [No other mention of the shock "two weeks later" has been found.] "Feb. 7: This morning about four o'clock we had a very noticeable and lengthy earthquake, which waked most of the Brethren and Sisters from sleep. In the evening between nine and twelve there was another distinct quake. We heard later that this extended over a wide area, especially in the southern and western parts of the United States, and that it caused no little fright in some places." (Mor. Recs. 7, p. 3166, Salem Diary.) "Feb. 7: In the morning at the fifth hour, and again in the evening between eleven and twelve o'clock, we felt such severe earthquake shocks that the room-doors in some of the houses were forced open." (Mor. Recs. 7, p. 3184, Bethania Diary.)

*1817: January 8, 0400 or 0500 hrs. Felt in the Winston-Salem area. "Jan. 8: In the fifth hour of the morning a slight earthquake was noticed in various places in the town and also in the neighborhood." (Mor. Recs. 7, p. 3352; Bethabara Diary.) "Dec. 11 [1817]: This afternoon I went with the children to Box Mountain and some of them got boxes. Recently an earthquake [probably that of Jan. 8] was felt there, though not severely." (Mor. Recs. 7, p. 3341; School Diary of Thomas Schultz of Salem.)

*1823: August 23, evening. Felt in the Winston-Salem area. "August 24: In Hope a Brother reported that last night on his farm he felt an earthquake, followed by a roaring noise that lasted a full minute." (Mor. Recs. 8, p. 3631; Salem Diary.) No other mention of this supposed earthquake has been found.

*1826: November 11, night. Felt in the Winston-Salem area. "May 12: Last night several persons living in and outside the town felt a slight earthquake shock." (Mor. Recs. 8, p. 3781; Bethabara Diary.) No other mention of this earthquake has been found.

1828: March 9, 2200–2300 hrs. Epicenter probably in Virginia. Reported as felt in Hillsboro, Raleigh, Milton, Charlotte, and Lincoln County in North Carolina, according to available contemporary newspapers. "Violent shock, Washington and Baltimore. Two shocks, lasting in all 30 seconds." (E. Hist.) [In *E. Hist.* the date is given as "Feb. 24 and Mar. 9".] "On Sunday night the 10th (*sic*) instant at ten minutes before 11 o'clock, a smart and distinct shock of an earthquake was experienced in this place [Hillsboro]. The writer was startled by a sound, like rumbling thunder, apparently not far off, and an instant cracking noise of the wainscoat of the room and an adjoining staircase, where he was sitting. . . . The direction of the sound appeared to be from the southeast to northwest. It continued but a moment of time." (*Hillsborough Recorder*, Mar. 19, 1828.) "March 10, 1828: Last night we felt an earthquake." (Mor. Recs. 8, p. 3862; Friedberg Diary.)

*1829: (?). Cherokee County, N. C. *A. J. S.* 109 (1875), p. 57, quoting a paper by the Hon. Thomas L. Clingman in the *Western Expositor* [original paper not

seen] says: "In the county of Cherokee, in the year 1829 or thereabouts, the Valley River Mountain was cleft open for a considerable distance during a violent shaking of the earth in that vicinity. The chasm, though partially filled up, is represented as still visible." This locality seems to have been south of Andrews, somewhere along the present Cherokee-Clay county border, not far from 35° 10′ N., 83° 50′ W. While it is just possible that this reference is to the March 9, 1828, earthquake, the localized effects described render this supposition very unlikely.

1833: August 27, 0615 or 0630 hrs. Central Virginia earthquake, reported from Raleigh, Tarboro, Halifax, Warrenton, etc. in North Carolina. "Summer of 1833, Central Virginia, few facts known, seems to have been a severe shock. Fences were shaken." (E. Hist.) Contemporary newspapers give the date as August 27, and the time as 6:15 or as 6:30 a.m. The shock was felt from Norfolk on the east to at least as far west as Lynchburg, and from Baltimore on the north to central North Carolina on the south. Near Richmond two negro coal miners were killed during a panic caused by this quake in one of the local coal mines. See also *B. S. S. A.* 3 (1913), pp. 128–129.

*1834: November 29, no time given. Felt in the Winston-Salem area. "Nov. 29: Some people noticed a slight earthquake." (Mor. Recs. 8, p. 4128; Salem Diary.) This is the last earthquake reported in the published volumes of the *Moravian Records*. The Salem area is probably no more seismic than the rest of the Carolina Piedmont but, because continuous diaries were kept by earthquake conscious people, we have many more slight ones reported from Salem than from elsewhere during the period covered by the records.

1843: January 4, 2130 hrs. Severe shock at Memphis, Tenn. (E. Hist.) Intensity 9. According to Berlen C. Moneymaker [personal letter], it was felt over much of North Carolina, although I have been unable to confirm this by reference to available contemporary newspapers. It was, however, felt both in Charleston, S. C., and in Augusta, Ga.

1843: February 8, 1040 hrs. "Great earthquake centering at Guadeloupe, W. I., and which appears to have been felt in the eastern part of the U. S., especially at Washington, D. C." (E. Hist.) Reported as felt from New Bern, Wilmington, Raleigh, Hillsboro, Fayetteville, Greensboro, Swift Creek, Salisbury, Martin County, and other places in North Carolina.

*1844 or 1845: June. Jackson County. *A. J. S.* 109 (1875), p. 57, quoting a paper by the Hon. Thomas L. Clingman in the *Western Expositor* [original paper not seen] writes: "In my former publication [letter to the *National Intelligencer*, Oct. 8, 1848] . . . I was soon informed that three or four years previously [previous to 1848 ?], in the southern part of Macon County, between the Tuckasegee River and the Cowee Mountain, the ground was shaken violently for several minutes. A few days afterward some persons discovered a fresh chasm, two or three feet wide, which extended more than a mile. This was in the month of June . . .". In his *Intelligencer* letter of 1848 Clingman mentions that these shocks were heard, but not *felt*, "in the town of Waynesville, some twenty miles off." This epicenter appears to have been located near what is now the three-way

corner of Macon, Swain, and Jackson Counties, the latter two not having been created at the time. It was probably in what is now Jackson County, and much less likely in what is now Swain County. It could not have been in the present Macon County, since it is said to have been located *east* of the Cowee Mountains, which now form the eastern boundary of Macon County. No mention of this earthquake has been found in any available contemporary newspapers.

1852: April 29, shortly before 1300 hrs. Reported from Raleigh, Greensboro, Hillsboro, and Milton in North Carolina. Epicenter probably in Virginia. "In p.m. in Washington and Baltimore, April 30, 1852." (E. Hist.) [The correct date, as given in contemporary newspapers, is April 29.] "*Earthquake.*—The shock of an earthquake was very sensibly felt by several persons at Raleigh, in this place [Hillsboro], and at Greensborough, on Thursday last the 29th ultimo, a little before one o'clock p.m. The *Greensborough Patriot* describes it as an undulatory motion, shaking the window sashes and rocking the furniture in the houses, and continuing four or five seconds, accompanied with a hollow rumbling noise. This description corresponds with the sensations felt here by the many persons who observed it." (*Hillsborough Recorder*, May 5, 1852.)

1861: August 31, a little after 0500 hrs. Felt in Raleigh, Charlotte, Wilmington, and other places in North Carolina, according to available contemporary newspapers. "Two shocks at Washington, D. C., at intervals of 5 minutes, lasting 10 seconds." (E. Hist.) Intensity 5. This epicenter was probably somewhere in Virginia.

*1874: February 10 to April 17. A protracted series of moderately strong (intensity 5 to 6) but strictly local shocks in McDowell County, N. C. This is undoubtedly the State's most famous earthquake, and much has been written concerning it. "Epicenter at about 35.7° N., 82.1° W. Local shocks, intensity 5–6. There were a series of explosive shocks, none severe, followed by deep rumbling noises. These were in the vicinity of Stone [and of "Rumbling Bald"] Mountain. At times stout log buildings shook violently. There were probably 50 to 75 shocks, each accompanied by rumbling, during the period named. Some of the explosions were described as like the rattling of artillery followed by a rumbling, the ground trembling for a few seconds after each explosion. The shocks were felt over an area 25 miles in diameter including Mount Mitchell. . . .The explosive shocks and noises were simultaneous. Shocks occurred on February 10 and 22, March 17 and 26, April 14 and 17." (E. Hist.)

See also: Smithsonian Report for 1874, "Series of Earthquakes in North Carolina," by Warren du Pre' Smith; "The Earthquake Scare in North Carolina," in *Popular Science Monthly* 13, p. 635, 1878; "Lecture Delivered Before the Washington Philosophical Society, by the Hon. Thomas L. Clingman, *A. J. S.* 109 (1874), pp. 55–58; *A. J. S.* 108 (1874), p. 79, with an account of a visit to this locality by F. H. Bradley; and the various State newspapers of the period.

There were more shocks in this area during January and February, 1880, and apparently also some slight repetition during January, 1884.

1875: December 22, 2345 hrs. Epicenter near Arvonia, Buckingham Co., Va. Reported as felt in Greensboro, Weldon, Raleigh, and Wilmington, in North

Carolina. "Epicenter near 37.6° N., 78.5° W. Was of force 7 or more, felt over 50,000 square miles." (E. Hist.) "Shock lasting twenty seconds at 11:45 p.m., from northeast to southwest, with rushing, roaring, noise, at Weldon, N. C. (M. W. R.). See also *B. S. S. A.* 3 (1913), pp. 129–130, and *A. J. S.* 112 (1876), p. 29.

*1877: April 26, 1700 hrs. "A slight shock was felt at Franklin, North Carolina, at 5 p.m., on April 26." (M. W. R.). See also *A. J. S.* 115 (1878), p. 23. No mention of this shock has been found in contemporary newspapers.

1877: November 16, 0238 hrs. Tennessee earthquake, felt at Murphy, N. C. "At Murphy, N. C., at 2:45 a.m., shock lasting fifteen seconds, from West to East." (M. W. R.) "At 0238, epicenter near 35.5° N., 84° W., force 5." (E. Hist.) See also *A. J. S.* 117 (1879), p. 158. No mention of this quake's having been felt in North Carolina has been found in contemporary newspapers.

*1878: November 23, 1000 hrs. "At Murphy, N. C., a slight shock at 10 a.m., from West to East, lasting one minute, not much jar, but a rumbling noise like distant thunder." (M. W. R.) See also *A. J. S.* 117 (1879), p. 162. Not mentioned in *E. Hist.* or in available contemporary newspapers.

*1879: December 12 and 13, 1900 and 0200 hrs. Felt in Charlotte and vicinity. "Two distinct shocks moving from West to East were felt in Charlotte, North Carolina, and in the surrounding country within a radius of 11 miles, the one at 7 p.m. of the 12th and the other at 2 a.m. of the 13th. The second was sufficiently distinct to rouse from sleep persons living in Charlotte, Sharon Township, Providence, and Pineville." (M. W. R.) See also *A. J. S.* 119 (1880), p. 299. Not mentioned in *E. Hist.* News stories in contemporary state newspapers, but no additional details given.

*1880: January 28, 29, and February 10. McDowell County. "Shocks and rumbling again reported from Bald Mountain, N. C." (A. J. S. 123 (1881), p. 199). No mention found elsewhere.

*1882: January 8, 1710 hrs. Felt at Cape Lookout, N. C. ". . . at 5:10 p.m., shock of about 10 seconds duration; house forcibly shaken, jarring windows and doors." (M. W. R.) See also A. J. S. 125 (1883), p. 355. Not mentioned in *E. Hist.* or in available contemporary newspapers.

*1882: October 15, 1230 hrs. Felt at Murphy, N. C. "On the 15th a slight shock of an earthquake occurred at this place at 12:30 p.m. The vibration was from south or southwest to north or northeast." (M. W. R.) See also *A. J. S.* 125 (1883), p. 359, where it is suggested that the true time might have been 12:30 *a.m.* [0030 hrs.] and the earthquake the Centralia, Illinois quake, which occurred about midnight that date. No mention that an earthquake of this date was felt in North Carolina has been found in contemporary newspapers. Not mentioned in *E. Hist.*

*1882: October 23, 0700 hrs. Felt in New Bern and Poloksville. "At about 7:00 a.m. a distinct shock, supposed to be that of an earthquake, was felt in this city [New Bern]. The shock was sufficient to shake houses, and was accompanied by a rumbling noise." (M. W. R.) "On Monday morning, at about 7 o'clock, a very distinct shock was felt in this city, supposed to be an earthquake.

Houses were shaken, and a rumbling noise was heard. Visitors from Poloksville say the same shock was felt there. We learn that New Bern has felt two or three shocks within the memory of the older inhabitants." (*New Bern Journal*, Oct. 24, 1882). See also *A. J. S.* 125 (1883), p. 359. Not mentioned in *E. Hist.*

*1883: September 21, 0645 hrs. Greensboro area. "Greensborough, N. C., 6:45 a.m. A heavy rumbling followed by a severe shake lasting one minute. Was most severe in the western portion of the town. There was much alarm, but no damage." (M. W. R.) See also *A. J. S.* 127 (1884), p. 363. Not mentioned in *E. Hist.* or in available contemporary newspapers.

*1884: January 18, about 0800 hrs. Felt in Wilmington, Beaufort, and vicinity. "Epicenter near 34.3° N., 78° W. Force 5 to 6." (E. Hist.) "Wilmington N. C.: A slight shock of an earthquake was felt at about 8 a.m. of the 18th. The shock was very perceptible, causing crockery etc. to shake. Reports from Fort Macon and Beaufort state that the shock was also felt at those places. . . . The duration of the shocks at Wilmington is estimated at from eight to thirty seconds. New River Inlet, N. C.: Two distinct shocks of earthquake were felt in this vicinity at 8:30 a.m. of the 18th. The shocks were separated by an interval of about two minutes, and were sufficient to displace crockery and to cause buildings, trees, etc. to vibrate. Fort Macon, N. C.: At about 7:50 or 7:55 of the 18th two slight shocks of earthquake were felt here and at Beaufort. The direction of the shocks was from southwest to northeast. They were of from three to four seconds duration, and accompanied by a rumbling noise." (M. W. R.) In *A. J. S.* 129 (1885), p. 427, it is stated that this quake was also felt ten miles east of New Bern and along the railroad connecting that city with Beaufort. Contemporary newspaper accounts say that at Beaufort the jar was sufficient to shift stovepipes and to unlatch doors.

*1884: January, no exact date given. McDowell County. The *Fayetteville Observer* concludes its account of the January 18th, 1884, quake with the remark: "This . . . lends probability to stories of the "trouble" at Bald Mountain. . . . By the way, the Morganton Mountaineer [no copies of this period available to the writer] reports more trouble in that quarter within the past week." No further mention of this occurrence has been found anywhere.

*1884: April 30, 0646 hrs. Ogreeta, Cherokee County. "At 6:46 a.m. of the 30th a low rumbling sound of earthquake, like rolling thunder, was heard; the noise apparently came from a point nearly due north of here." (M. W. R.) See also *A. J. S.* 129 (1885), p. 428, which notes that no tremors were reported. No other mention of this occurrence has been found.

*1884: "Summer". Elk Mountain, near Asheville. The *Orange County Observer*, for Sat., Sept. 5, 1885, in a story on the August 6, 1885, Watauga County earthquake, says: "There was a similar shock at Elk Mountain, near Asheville, last summer." This is presumably the summer of 1884, rather than that of 1885. The "Elk Mountain" mentioned is probably the Elk Mountains which are located just northeast of Asheville, at about 35° 40′ N., 82° 30′ W. No other mention of this shock has been seen anywhere.

*1885: August 6, 0800 or 0900 hrs. Watauga County. Felt at Boone, Banner

Elk, Blowing Rock, on Grandfather Mountain, etc. The exact date of this quake is questionable. Although *E. Hist.* and most other references give it as August 13, a study of the contemporary newspaper accounts indicates that it was most probably on the 6th, the difficulty arising from the fact that most of the papers in which it was mentioned were weeklys so that one week's error in dates is easily produced by careless editing. "Epicenter near 36.2° N., 81.6° W. Blue Ridge Mountains, Wautega (*sic*) County, N. C. Noise like thunder at Boone. Intensity 4–5. (E. Hist.) "There were violent shocks of earthquake last Thursday in the Blue Ridge Mountains in Watauga County. At first there were noises like thunderclaps, . . . then the earth shook, and terrible noises were heard. . . . The noises and shocks were felt at Boone." (M. W. R.) The *Lenoir Topic* for Aug. 19 and Aug. 26, 1885, says in part: " . . . Mrs. Ried, who lives . . . about 2½ miles from Blowing Rock, was sitting in the house and was surprized to hear a very loud clap of thunder, although the sky was perfectly clear, and immediately the house began to shake, dishes to rattle, and a noise was heard as though 'a six-horse team was being driven rapidly through the house.' It lasted but a few moments, but during the time of it there was a perceptible and violent rocking. Mrs. Ried says she . . . could hardly stand. . . . It made its debut about 8 or 9 o'clock in the morning. We are informed that it was felt all over Watauga County, especially at high points. It seems, however, to have been more severe along the backbone of the Blue Ridge."

1886: August 31, Charleston, S. C. Two main shocks at 2151 and 2159 hrs., followed by at least two aftershocks which were also felt in North Carolina, causing great alarm. Damage in North Carolina very light, confined to chimneys, a few brick walls, fallen plaster, broken dishes, etc. Church bells rang in a few places, rumbling noises were common. Felt most severely in the eastern portion of the state. "Shocks as severe at Raleigh, 215 miles away, as at Wilmington, 152 miles away." (E. Hist.) Since there are so many comprehensive accounts of this earthquake generally available, it will not be further described here.

1886: September. During this month many aftershocks of the Charleston earthquake were felt in various parts of North Carolina. Most of these are listed in *M. W. R.* for Sept., 1886.

1886: October 22, about 0500 and 1445 hrs. "Strong shocks at Charleston; the first in the morning felt with force 7 in Charleston, Atlanta, Augusta, and elsewhere, and the second with force 8 at Summerville, S. C., felt at Washington, Richmond, Louisville, and elsewhere." (E. Hist.) North Carolina newspapers reported that these shocks were felt in such places as Salisbury, Fayetteville, Lenoir, New Bern, Wilmington, Kinston, Graham, Pittsboro and the like. In other words, generally throughout the state.

1895: October 31, 0508 hrs. Earthquake at Charleston, Mo. Felt at Charlotte, Lenoir, Skyuka, Waynesville, Raleigh, Oxford, and other places in North Carolina. "Epicenter at 37.0° N., 89.4° W., intensity 8–9, felt from Canada to Mississippi and Louisiana, and from Georgia and Virginia to Kansas and South Dakota. Considered the hardest shock in the region since the New Madrid earthquakes of 1811 and 1812." (E. Hist.)

*1896: February 10 or 12, 2045 hrs. Felt at Oxford and Hillsboro and vicinity.

Of the available contemporary accounts, three indicate that the quake was on Wednesday the 12th and two others that it was on Monday the 10th: It is not probable that we are dealing with two separate earthquakes, since the conflicting dates are found in connection with identical news items in the various state papers. "Oxford N. C., Feb. 13:—Quite a severe earthquake was felt here last evening at 8:45 o'clock. Windows and doors rattled, and there was the usual waving motion accompanied by a rumbling noise, that seemed to go from southeast to northwest." (*Raleigh News and Observer*, Feb. 14, 1896.) "A great many people in Hillsboro and the surrounding country are confident that they felt the shock of an earthquake Monday night between half past 8 and 9 o'clock" (*Orange County Observer*, Feb. 15, 1896).

1897: May 3, 1218 hrs. Pulaski City, Va. Reported as felt in Lenoir, Winston-Salem, Graham, Elkin, and other North Carolina localities. "Epicenter at 37.1° N., 80.7° W., intensity 7, felt over 150,000 square miles." (E. Hist.) "A very perceptible earthquake was felt here and in the county on Monday [May 3]. Two shocks were noticed—one at 12:16 (*sic*) and another two or three hours later in the day. Today's papers speak of its being felt very generally over the state." (*Lenoir Topic*, May 4, 1897.)

1897: May 31, 1358 hrs. Giles County, Va. Generally felt throughout North Carolina, accompanied by roaring noises. "In Raleigh two shocks were reported, each lasting 30 seconds, and chimneys were thrown down." (M. W. R.) "Epicenter at 37.3° N., 80.7° W., intensity 8–9, felt over 280,000 square miles from Georgia to Pennsylvania, and from the Atlantic Coast to Indiana and Kentucky." (E. Hist.)

1897: October 21, 2220 hrs. Wytheville, Va., generally felt in central and western North Carolina, including Burlington, Winston-Salem, Lenoir, etc. "Epicenter near 36.9° N., 81.1° W., intensity 5–6, felt over 20,000 square miles." (E. Hist.) "Winston, N. C., Oct. 22:—There was a distinctive earthquake shock here about half past ten o'clock last night. It made windows rattle for a few seconds. The wave appeared to pass from west to east and seemed to be two waves in very close succession." (*Raleigh News and Observer*, Oct. 23, 1897.) See also *M. W. R.* for the month.

1898: February 5, about 1500 hrs. Epicenter probably in Virginia. Felt in North Carolina, according to contemporary newspapers, at: Roxboro, Raleigh, Lenoir and "other parts of Caldwell", Statesville, and Marion. Not mentioned in *E. Hist.* "The earthquake which shook many of the eastern states last Saturday, and was felt in the western part of this State, was also felt here. . . . The vibrations were distinct, lasting about three seconds and shaking windows in houses." (*Raleigh News and Observer*, Feb. 10, 1898.)

*1898: February 10, 2330 hrs. Local tremor at Raleigh, N. C. The only mention I find of this tremor is a story in the *Raleigh News and Observer* for Feb. 12, 1898: "An earthquake shock was felt in Raleigh Thursday night at 11:30 o'clock. It was quite distinct and lasted about twenty seconds. In reporting it to the Weather Bureau in Washington, Mr. Von Herrman, the local forecaster here, put it down as an "earth tremor" rather than an earthquake."

1898: November 25, 1500–1515 hrs. Virginia earthquake, felt in North Caro-

lina at Winston-Salem, Franklinsville, Charlotte, Raleigh, Graham, Pittsboro, and other localities. See *M. W. R.* "Two distinct earthquake shocks were felt here [Raleigh] Friday, Nov. 25 afternoon between 3 and 3:15 o'clock. The first shock was more violent than the second. It lasted about five seconds. Neither of the shocks was of such violence as to do any harm. As a rule only people in tall buildings detected that anything was wrong. From here the disturbance seems to have passed westward." (Quoted from the *Raleigh News and Observer* by the Graham *Alamance Gleaner*, Dec. 1, 1898). The *Gleaner* further states that "A very distinct earthquake shock was felt here [Graham] at 3:04 last Friday afternoon. . . . 'Squire Glendenin . . . was upstairs in the Oneida Store among the tinware and crockery and it rattled at such a lively rate that he was induced to get down rather hastily . . .". This quake is not mentioned in *E. Hist.*

1899: February 13, 0430 hrs. Lynchburg, Va. Felt in North Carolina at such places as Mount Airy, Charlotte, Winston-Salem, Elkton, etc. in the western part of the state. "Epicenter near 37° N., 81° W., intensity 5–6, felt over 30,000 square miles." (E. Hist.) "Winston-Salem, Feb. 13:—Many citizens were awakened at 4:30 this morning by four severe earthquake shocks which lasted several seconds. The vibrations were from southeast to northwest. Many think it was the severest and most distinctive shock yet felt in this section." (*Charlotte Daily Observer*, Feb. 14, 1899.)

*1911: April 20 or 21, 2200–2300 hrs. Another very indefinite date. *E. Hist.* gives it as "April 21 & 22", available contemporary newspapers variously as "the 20th", "night of the 20–21st", "the 21st", etc. The most probable date seems to be the 20th. "Caeser's Head, N. C. (*sic*). Epicenter at about 35.2° N., 82.7° W., intensity 5, felt over 600 square miles. Along the Blue Ridge. Cracks opened. Felt at Hendersonville, 15 miles northeast." (E. Hist.) The given epicenter is in North Carolina, but Caeser's Head, despite statements in the *Associated Press* news dispatches and in *E. Hist.*, is across the border in South Carolina. At Hendersonville the quake was described as "a long rolling detonation, a trembling of the earth felt throughout Henderson County and said to extend as far south as Spartansburg, S. C." (*Charlotte Daily Observer*, Apr. 23, 1911). According to other newspaper accounts it was also felt in Asheville, where a "slight trembling and a roaring noise" are mentioned.

1912: June 12, 0530 hrs., Summerville, S. C. "Epicenter at about 32.9° N., 80.0° W., intensity 7, felt over 35,000 square miles. Felt at Wilmington, N. C." (E. Hist.) See also *B. S. S. A.* 4 (1914), pp. 145–146. According to contemporary newspapers, it was felt by a large number of people in Wilmington, and some were awakened by the shock which shook houses. No damage was done. In Charlotte it was reported that windows and dishes rattled. Some reports from both Wilmington and Charlotte mention three distinct shocks in close succession.

1913: January 1, 1328 hrs. Union County, S. C. "Epicenter near 34.7° N., 81.7° W., intensity 8, felt over 43,000 square miles. Quake was felt at Raleigh, more than 200 miles away." (E. Hist.). See also *B. S. S. A.* 3 (1913), pp. 6–13, where an isoseismal map is given. At Raleigh the shock is said to have lasted thirty seconds. In available contemporary newspapers some ten or twelve North

Carolina towns are said to have felt the shock, including Asheville, Bessemer City, Davidson, Gastonia, Greensboro, King's Mountain, Salisbury, Shelby, and Statesville. No damage seems to have been done in North Carolina except at King's Mountain, where one chimney was thrown down.

1913: April 17, 1130 hrs. East Tennessee. "Epicenter at about 35.3° N., 84.2° W., intensity 5–6, felt over 3,500 square miles, including western N. C." (*E. Hist.*) *E. Hist.* gives the time as 11:30 p.m., but contemporary accounts indicate that it was 11:30 a.m. See also *B. S. S. A.* 3 (1913), pp. 193–194. "Brasstown, N. C., April 19:—A slight but exciting earthquake shock was felt here about noon Thursday [the 17th] which lasted about thirty seconds." (*Raleigh News and Observer*, Apr. 20, 1913.)

1914: March 5, 1505 hrs. 30 miles southeast of Atlanta, Ga. "Epicenter at about 33.5° N., 83.5° W., intensity 6, felt over 50,000 square miles. Was felt in western N. C." (E. Hist.) See also *B. S. S. A.* 4 (1914), p. 44 and *B. S. S. A.* 5 (1915), pp. 96–99. "March 7, 1914:—Several persons in offices on the 10th floor of the Commercial National Bank Building [in Raleigh] stated yesterday that they felt the slight tremor of an earthquake. . . . this is the first report of any disturbance detected in North Carolina." (*Raleigh News and Observer*, March 7, 1914.) No other references to this quake's having been felt in North Carolina have been found.

*1915: October 29, Marshall, N. C. Times given in various accounts do not agree, i.e., 0025 hrs., 0035 hrs., 0125 hrs. *E. Hist.* gives it as 2300 hrs., perhaps a typographical error for 0023 hrs. "Epicenter at about 35.8° N., 82.7° W., intensity 5, felt over 1,200 square miles. People awakened at Marshall and at Asheville." (E. Hist.) See also *B. S. S. A.* 5 (1915), p. 238, and *B. S. S. A.* 6 (1916), pp. 218–226, where it is stated that two distinct shocks were felt, about two minutes apart, strong enough to shake houses and awaken many people. No additional information has been found in available contemporary newspapers.

*1916: February 21, 1739 hrs. Skyland, N. C. "Epicenter at about 35.5° N., 82.5° W., intensity 7, felt over 200,000 square miles. In Appalachian Mountains near Skyland, N. C., not far from Asheville. Was felt from Georgia to Virginia, and as far west as Alabama, Tennessee, and Kentucky. The most distant point where it was felt was Norfolk, Va., 365 miles away. Sounds were heard throughout the area included within isoseismal 4. Within 200 miles of the epicenter crockery fell from shelves . . . In a few places plaster was cracked. No important damage anywhere." (E. Hist.) See also accounts in *B. S. S. A.* 6 (1916), pp. 218–226, *B. S. S. A.* 6 (1916), p. 50, and *M. W. R.* 55 (1916), p. 154. The account in *B. S. S. A.* 6, pp. 218–226, gives the epicenter as 35° 35′ N., 83° 05′ W., and the *M. W. R.* account places it at 35° 30′ N., 82° 30′ W. In the *M. W. R.* account, 37 different North Carolina communities are listed as having felt this quake, distributed pretty generally throughout the state. This earthquake, one of the very largest which has occurred within the borders of North Carolina during historic times, was instrumentally recorded at Cambridge, Mass.; Buffalo, N. Y.; Lawrence, Kans.; St. Louis, Mo.; Georgetown, Md.; and Washington, D. C., according to the *M. W. R.* account.

*1916: August 26, 1436 hrs. Western North Carolina. "Epicenter at about 36°

N., 81° W., intensity 5, felt over 3,800 square miles." See also *M. W. R.* 44 (1916), p. 483, which states that the epicenter was a little to the northeast of that of the quake of Feb. 21, 1916. See also *B. S. S. A.* 6 (1916), p. 224, where it is stated that the highest intensities were recorded from Statesville and Taylorsville. North Carolina towns mentioned in various accounts, including available contemporary newspapers, are: Harmony, Lenoir, Lincolnton, Morganton, Newton, North Wilkesboro, Statesville, Taylorsville, Hickory, and Conover. No damage seems to have been done anywhere.

1916: October 18, 1604 hrs. Easonville, Alabama. "Epicenter near 33.5° N., 86.2° W., felt over 100,000 square miles. Was felt from North Carolina to Mississippi, and from Georgia to southern Indiana." (E. Hist.) See also *B. S. S. A.* 6 (1916), p. 238, where no mention of effects in North Carolina is made. Also *M. W. R.* 44 (1916), pp. 590, 690, where it is said to have been felt in Highlands, Murphy, and Nantahala in this State. News stories in most of the State papers; no mention seen of effects in North Carolina.

1918: April 9, 2109 hrs. Middle and northern Virginia. "Epicenter near 38.7° N., 78.4° W., intensity 8, felt over 100,000 square miles. Felt at Roanoke City (?) N. C." (E. Hist.). See also *B. S. S. A.* 8 (1918), p. 90 and *M. W. R.* 46 (1918), pp. 189, 594. The reference to "Roanoke City, N. C." (Roanoke Rapids?) may be in error, since no other reference to this quake's being felt in North Carolina has been found.

*1920: Various times. Stokes County, N. C. The *New York Times* for Jan. 23, 1921, carries the following news item:

> "Winston-Salem, N. C., Jan. 22.—An investigation of Flat Shoal Mountain was demanded today by residents of Stokes County, this state. Dwellers in the vicinity charge that it has rumbled and growled at intervals for a year, wrecking their peace of mind. The sound was like distant blasting, they said, and evergreens and trees on the mountain were dying.
>
> "Fearing that they might have a caged volcano to deal with, the citizens asked that Government earthquake sharps be sent to look into the disturbance."

This sounds rather like the occurrences in McDowell County, in 1874. No other mention of this particular phenomenon has been found elsewhere.

*1924: October 20, 1530 hrs. Western North Carolina. "Epicenter near 35° N., 82.6° W., intensity 5–6, felt over 56,000 square miles. At epicenter buildings were shaken and furniture overturned. A loud roar accompanied the shock." (E. Hist.) See also *Q. S. R.* for 1924–25, where the epicenter is given as "Pickens Co., S. C." This quake, according to available information, was felt in North Carolina at: Asheville, Brevard, Charlotte, Hendersonville, Murphy, and in the adjacent areas, with the greatest disturbances at Hendersonville and Brevard. *B. S. S. A.* 14 (1924), pp. 223–229, states that this shock was not recorded on any seismograph then in operation. Ten reports mentioned two separate shocks. See also *B. S. S. A.* 14 (1924), p. 274.

*1926: July 8, 0450 hrs. Southern Mitchell County, N. C. "Epicenter near 35.9° N., 82.1° W. "Felt by few: few alarmed: cracks in ground: houses rattled,

chimneys cracked, underpinnings of buildings cracked: chimney fell NE to SW: water pipeline broken: glassware displaced. Abrupt swaying NE-SW. Disturbed area ½ mile long, 300 yards wide, several houses moved on their foundations and damaged. Shock said to have been felt six miles away." (Q. S. R., July–Aug.–Sept., 1926, quoting "Report to State Geologist by Prof. Collier Cobb".) No other mention of this earthquake has been found. The notation "Felt by few: alarmed few" is puzzling in view of the further description of the local effects. Probably "only a few" felt it because it affected such a small area but, within this area, almost everyone must have been at least aware of the quake, if not downright alarmed by it!

*1927: October 27. "At an early hour". Elizabeth City, N. C. "Felt by many, many alarmed. There were three shocks a few seconds apart; doors and windows rattled." (Q. S. R., Oct.–Nov.–Dec., 1927.) Not mentioned in *E. Hist.* See also *B. S. S. A.* 17 (1927), p. 258, where it is stated that the shock caused great excitement in Elizabeth City, and the above data were repeated. No other mention of this quake has been found.

*1927: November 22, 1950 hrs. Southport, N. C. "Felt by many; five shocks; windows rattled; some panic; possibly blasting." (Q. S. R., Oct.–Nov.–Dec., 1927.) A dispatch in the *Greensboro Daily News* for Nov. 23, 1927, says:

> "Southport, N. C., Nov. 22.—Five distinct shocks between 6:50 and 7:00 p.m. were felt tonight. They were of slight intensity . . . no damage was done . . . in many sections of town the shocks were noticed by only a few. . . . In many sections of town residents left their homes as the 3rd, 4th, and 5th shocks rattled dishes and windows. . . . Efforts have been made to account for the shocks, but marine officials know of no gun firing off the coast and no blasting has been in process in the neighborhood. . . . The shock was not felt in Wilmington."

Other State papers carry identical news items.

*1928: November 2, 2303 hrs. Asheville, N. C., area. "Epicenter near 36.0° N., 82.6° W., intensity 6, 40,000 square miles. Reported as felt in some twenty North Carolina communities (which are listed)." (U. S. E. 1928, pp. 6–9). See also *B. S. S. A.* 18 (1928), pp. 243–245, 287, and *Proc. G. S. A.* (1934), pp. 446–447. *E. Hist.* describes it as being centered near the northeast border of Tennessee, or in adjacent North Carolina, and as chiefly felt along the French Broad River from Asheville to Newport. There was some slight damage at Asheville in upper stories of buildings, where bookcases were upset and walls cracked. A mild panic was created in one theater. Some floors were cracked, dishes thrown from shelves, and a heavy safe moved on its rollers. Several reported two shocks. In some places, as at Elkin, thunder-like noises preceded the shock. Was felt as far east as Winston-Salem.

*1928: November 19, 2245 hrs. Asheville, N. C., and Johnson City, Tenn. "Epicenter near 35.8° N., 82.3° W. Felt over 10,000 square miles. Probably an aftershock of the earthquake of November 2. Felt with most force in West Asheville along the French Broad River, and at Hot Springs, N. C. and Erwin Tenn. No damage." (U. S. E. 1928.) Not mentioned in *E. Hist.* See also *B. S.*

S. A. 18 (1928), p. 288. Generally mentioned in the State papers, where the shock was described as "slight."

*1928: November 22, no time given. Wilmington and Southport, N. C. "Epicenter near 34° N., 78° W." (U. S. E. 1928). Not mentioned in *E. Hist.* or in any available State papers.

*1928: December 22, 2130 hrs. Charlotte, N. C. "Epicenter near 35.3° N., 80.3° W. Distinct rumble and shake felt; strongly felt at County Home and at Mecklenburg County Industrial Home." (U. S. E. 1928.) Not mentioned in *E. Hist.* See also *B. S. S. A.* 18 (1928), p. 291. An item in the *Charlotte Observer*, Dec. 23, 1928, says, in part: "One short distinct rumble . . . shook structures and rattled pictures on the walls . . . was reported from numerous residents of the county home and the Newell and Back Creek sections northeast of the city. . . . One man at the county home said 'it sounded like the whole corner of the building was getting ready to fall in'."

*1935: January 1, 0315 hrs. North Carolina-Georgia border. "Epicenter near 35.1° N., 83.6° W., intensity 5–6, felt over 7,000 square miles. Slight damage at Dahlonega, Ga., and at Almond and Gay in N. C." (E. Hist.). *U. S. E.*, 1935, reports that it was felt in 23 North Carolina communities, which it lists. According to *B. S. S. A.* 25 (1935), pp. 247–251, there was one shock at most places, but at Franklin three at intervals of several seconds, preceded by a rumbling. Except at Franklin, the noises followed the shock. Not recorded at any seismological station.

1935: November 1, 0104 hrs. Timiskaming, Can. (E. Hist.) According to *U. S. E.*, 1935, was reported as felt at Louisburg, N. C., but this is probably an error, since it is the only report from south of central Virginia.

*1936: January 1, about 0300 hrs. "Epicenter near the Georgia-North Carolina border, between Murphy, N. C. and Blue Ridge, Ga. In North Carolina was felt only at Murphy. Intensity 3." (U. S. E. 1935.) See also *B. S. S. A.* 26 (1936), p. 177, where it is stated that the epicenter of this quake was 35 miles from that of Jan. 1, 1935, which was of intensity 5. Not mentioned in *E. Hist.*, and no mention found in contemporary newspapers.

*1936: September 6, no time given. Albemarle, N. C. "Albemarle, N. C., Sept. 6.—A slight tremor was felt here, which caused no damage." (B. S. S. A. 26 (1936), p. 392.) Not mentioned in *E. Hist.* or in available contemporary newspapers.

*1938: March 31, 0510 hrs. North Carolina-Tennessee border. "A shock of intensity 3 to 4 was felt over an area extending from Knoxville, Tenn., to Asheville, N. C." (U. S. E. 1938.) No further mention of this supposed earthquake has been found elsewhere.

*1940: December 24, 2050 hrs. Asheville, N. C. "Very light shock" (U. S. E. 1940). For mention in State papers see accounts of earthquake of Dec. 25, 1940. Not mentioned in *E. Hist.*

*1940: December 25, 0149 hrs. "Weak earthquake felt at Honeycutt and at Asheville, N. C. Recorded on the seismograph at Cincinnati." (U. S. E. 1940). According to contemporary newspapers, there were two distinct shocks felt at

Asheville, the first shortly before 9 p.m. on December 24, and the second at 1:50 a.m. on the 25th. Witnesses likened the occurrence to that which might be caused by the passing of a heavy truck and said it was followed by a distinct "boom" sound. No damage was reported. Described in *B. S. S. A.* 31 (1941), p. 177. Generally reported in the State papers and in the *New York Times* for Dec. 26th. Not in *E. Hist.*

*1941: May 10, 0612 hrs. Asheville, N. C. "Slight shock felt in northern and western parts of the city." (U. S. E. 1941). *B. S. S. A.* 31 (1941), p. 268, says that windows and dishes rattled in Asheville. Not in *E. Hist.* or any available contemporary newspapers.

1945: July 26, 0623 hrs., 03 secs. Thirty miles northwest of Columbia, S. C. "Epicenter near 34.3° N., 81.4° W., intensity 6, felt over 25,000 square miles. No damage. Many reported rumbling noises preceding the earthquake. Felt, with intensity 4, at Asheville and at Charlotte, N. C." (U. S. E. 1945). A friend of the writer reports that he felt it in Morganton, N. C. According to the *Charlotte Observer* for July 27, 1945, doors and windows rattled in that city and some few were awakened. A few reported a growling or grumbling noise, likening it to the sound and feel of a distant explosion or the firing of a large gun. *E. Hist.* locates the epicenter as at Murray Lake, S. C., but gives no time.

1950: June 18, 2319 hrs. Alcoa, Tenn. "Rapid trembling motion felt by many. Loose windows rattled. Was felt in Knoxville, Marysville, etc. in Tenn., and as far as Tapoco, N. C. In the last named place reporters stated jars and cans on shelves were displaced." (U. S. E. 1950). No mention found in available state papers.

1954: January 1, about 0925 hrs. East Tennessee. A large area east and north of Knoxville, Tenn. was affected. In Asheville, N. C., houses were shaken, according to newspaper accounts. A professional geologist reports that he felt it in Shelby, N. C., the most eastern point from which a positive report was received. No damage anywhere. Was recorded by the seismograph in Chapel Hill at 0926 hrs.

1955: April 21, about 0208 hrs. Earth tremors were felt over much of Piedmont North Carolina which were not caused by a true earthquake, but by the shock waves of a large fireball meteor which passed across the state. The seismograph at Chapel Hill recorded them at 0208 hrs. Occurrence described in *E. Notes* 26 (1956), p. 20. Compare events of Aug. 11, 1792.

*1955:[1] September 28, about 0201 hrs. North Carolina-Virginia border. Epicenter near 36.6° N., 81.3° W., intensity 4–4½, felt over about 1700 square miles. Reported from 21 communities in North Carolina and Virginia. Felt throughout most of Ashe and Alleghany Counties. Two shocks, about one minute apart, accompanied by a rumbling noise. Houses creaked, windows and dishes rattled, some few persons awakened. Recorded on the seismograph at Chapel Hill at 0202 hrs. Described in *E. Notes* 27 (1956), pp. 1–2.

1956: September 7, about 0840 and 0853 hrs. Two mild shocks affecting eastern

[1] Previously reported as 1956, in error (Jour. Elisha Mitchell Sci. Soc. 72: 274).

Tennessee, western North Carolina, and adjacent parts of Kentucky. Recorded on seismographs at St. Louis, Mo.; Columbia, S. C.; Columbia University, N. Y.; and at Chapel Hill, N. C. These shocks were felt in the following places in North Carolina, according to information collected by Moneymaker (Berlen C. Moneymaker, personal letter) and the writer: Asheville, Canton, Franklin, near Waynesville, Andrews, Bryson City, Fontana Dam, Mars Hill, Robbinsville, Sylva, Tapoco, etc. At the time of writing, the epicenter has not been instrumentally located, but Moneymaker (personal letter) places it near 36° 20′ N., 83° 45′ W., calling this an "approximate and tentative" location. The shocks were generally accompanied by rumbling noises. No damage seems to have been reported anywhere. Generally described in the State newspapers.

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THE PREPARATION OF o-DIMETHOXYBENZENE

By John B. Gallent and John M. Stewart[1]

Department of Chemistry, Davidson College, Davidson, North Carolina

In preparing a series of ethers from the isomers of dihydroxybenzene, o-dimethoxybenzene (veratrole) was prepared by the methods of Ullmann (1903) and of Perkin and Weizmann (1906).

[1] Present address: Rockefeller Institute for Medical Research, New York, N. Y.

Ullmann directed that 0.1 M. of o-dihydroxybenzene be treated with 50 ml. of 20 per cent sodium hydroxide (0.25 M.) followed by the addition of 20 ml. (0.2 M.) of dimethyl sulfate. The mixture is cooled after the reaction is complete and the veratrole is extracted with ether and recovered by vacuum distillation. The yield reported by Ullmann was 83 per cent. When we prepared veratrole using the method of Ullmann outlined above and using 0.5 M. of o-dihydroxybenzene, 250 ml. of 20 per cent sodium hydroxide and 1.0 M. of dimethyl sulfate we obtained yields of from 50 to 69 per cent.

In the method of Perkin and Weizmann a solution of 100 gms. (0.909 M.) of o-dihydroxybenzene in 200 ml. of methyl alcohol is prepared. 75 gms. (0.5 M.) of dimethyl sulfate are added and the solution is cooled to $-5°$ C. A solution of 150 gms. of potassium hydroxide in 350 ml. of water is prepared and is added to the cold mixture. Perkin and Weizmann claimed that, when the potassium hydroxide solution was added, a "vigorous" reaction occurred and the methylation was complete in three minutes. These authors reported an almost quantitative yield, i.e., 95 to 96 per cent. Following this method and using the amounts of materials called for above, we obtained yields of from 6.6 per cent to 12.5 per cent. No vigorous reaction was observed during the addition of the potassium hydroxide solution.

Lewis, Shaffer, Trieschmann and Cogan (1930) established what they considered to be the most effective conditions for the methylation of phenol by dimethyl sulfate. Using 0.2 M. of phenol, 0.1 M. of dimethyl sulfate, 0.2 M. of sodium hydroxide and 0.3 M. of water, and heating the mixture for five hours, they were able to obtain 90 per cent of anisole. Using the same quantities but heating for only one hour produced a yield of 70 per cent anisole. The mixtures were not stirred.

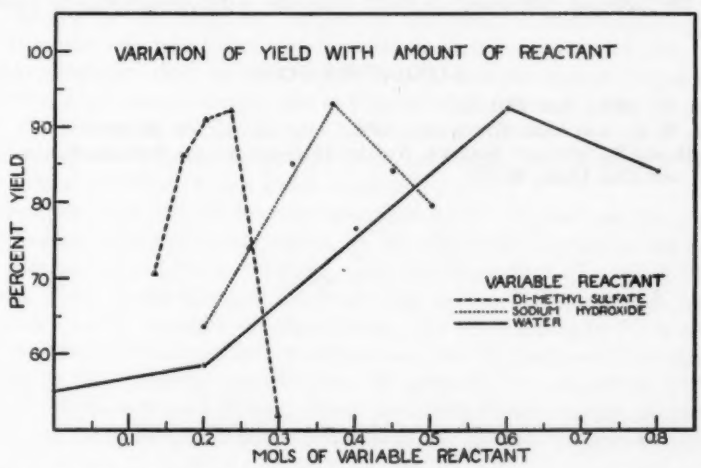

FIG. 1. Variation of yield of veratrole with concentration of water, sodium hydroxide and dimethyl sulfate.

In our study of the preparation, we ran a series of experiments using 0.1 M. of o-dihydroxybenzene and holding two of the reagents, sodium hydroxide, dimethyl sulfate and water, constant while the third was varied. Using this method we obtained our best yield of veratrole (Fig. 1) when 0.1 M. of o-dihydroxybenzene was added to 0.3 M. of solid sodium hydroxide in a 200 ml. flask equipped with a reflux condenser; 0.6 M. of water was added to the solids in the flask. When the water was added, the sodium hydroxide and the o-dihydroxybenzene reacted to form the sodium salt of o-dihydroxybenzene. In all experiments the mixture was heated 15 minutes to assure maximum salt formation. 0.2 M. of dimethyl sulfate was added to the solids in the flask; a dropping funnel was used and the dimethyl sulfate was added dropwise. The reaction of the sodium salt of o-dihydroxybenzene with dimethyl sulfate is violent and it was necessary to shake the flask at regular intervals. If the reaction became dangerously violent, the flask was cooled in an ice bath. When all of the dimethyl sulfate had been added the mixture was refluxed for one hour. Using this method and the amounts of materials indicated, we obtained yields of from 90 to 93 per cent of veratrole (B. pt. 88°/5 mm). In running larger batches, we used 0.5 M. of o-dihydroxybenzene, 1.5 M. of sodium hydroxide, 3.0 M. of water to which was added 1.0 M. of dimethyl sulfate. Yields of from 82 to 87 per cent were obtained. In running batches of this size, a 500-ml. three-necked flask fitted with reflux condenser, dropping funnel and motor-stirrer was used. The dimethyl sulfate addition required one hour and the mixture was refluxed for one hour.

The following general conclusions concerning the dimethylation of o-dihydroxybenzene may be drawn: (a) satisfactory yields will be obtained only when a minimum amount of water is used to assure a maximum concentration of sodium salt of the dihydroxybenzene and (b) an excess of sodium hydroxide above the amount calculated to react with the o-dihydroxybenzene must be present.

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DIDYMOSAMAROSPORA, A NEW GENUS OF FUNGI FROM FRESH AND MARINE WATERS[1]

By T. W. Johnson, Jr., and Harvey S. Gold

Department of Botany, Duke University, Durham, North Carolina

Fungi occurring on the stems and leaves of phanerogams in intertidal regions have been almost entirely neglected. Cooke (1877), Ellis and Everhart (1885), and more recently, Johnson (1956), have reported fungi from such phanerogams. The fungus flora supported by living or dead tissue of angiosperms which may only occasionally be subject to submersion in saline water, similarly, is incompletely known. Fungi occurring on intertidal or tidewater hosts are of particular interest since these parasites or saprobes must have considerable tolerance to periodic submersion in sea water. Some fungi occur on phanerogams which are subjected to fluctuating gradients of salt and fresh water; these fungi probably have a marked degree of adjustment to salinity changes. The latter group of fungi are significant in terms of the establishment of criteria for their designation as "marine", "brackish water", or "freshwater" forms.

Several instances of the occurrence of so-called "marine" species of fungi both in sea water and in freshwater have been recorded (unpublished notes). These observations have led naturally to a detailed consideration of the distribution of fungi in a continuous body of water ranging in salinity from 0.0‰ to 35+‰. One such area in the Beaufort, North Carolina, region, is Mullet Pond, on Shackleford Banks. The western end of the pond is freshwater except for a time subsequent to periods of extreme high tides such as occur during hurricanes. The northeastern drainage of this pond is subject to tide flush twice a day, hence the salinity in the northern portion of the pond is maintained at a level equal to that of the surrounding bay. Studies are in progress on this pond on fungal population shifts as influenced by salinity changes. Several fungi have been collected which are apparently new to science. Among these is a fungus combining the characteristics of the genera *Samarospora* Rostrup and *Samarosporella* Linder, yet which is clearly distinct from these taxa. This paper is a report on this fungus, for which a new genus is erected.

Samarospora potamogetonis was described as it occurred on the pondweed *Potamogeton natans* (Rostrup, 1893a, b). The distinctive feature of the fungus is the presence of a hyaline, irregular, wing-like appendage on each of the ascospores. There are no figures to illustrate these spores. The spores of *S. potamogetonis* are hyaline, nonseptate, long-cylindric, and 12–14 μ long by 5 μ in diameter. Asci are described as globose or subglobose, and eight-spored. Paraphyses are lacking in the spherical, non-ostiolate, olivaceous-brown, superficial perithecia. Linder (Barghoorn and Linder, 1944) described *Samarosporella pelagica* from driftwood. As in Rostrup's monotypic genus, the hyaline, nonseptate ascospores

[1] The engraving for the figures was supplied by the authors.

of *S. pelagica* each possess an irregular, colorless, gelatinous sheath. *Samarosporella pelagica* differs principally from *Samarospora potamogetonis*, however, in that the perithecia are ostiolate, and the asci are fusoid to somewhat rostrate. From a comparison of the generic and specific descriptions of these fungi, other, less conspicuous differences are apparent. The ascospores of Linder's species are considerably larger than those of *Samarospora potamogetonis*, and are elongate-ellipsoid; the perithecia are black and innate. In common with Rostrup's species, *Samorosporella pelagica* lacks paraphyses. The fungus from Mullet Pond, while obviously very similar to these two taxa, possesses certain features which preclude its inclusion in either of the known genera.

Didymosamarospora gen. nov.

Perithecia nigra vel atro-brunnea, carbonacea, innata, subglobosa, ostiolata; paraphysibus sparsis. Asci lato-cylindricales vel lato-clavati, deliquescentes, sporis 4 usque ad 8. Ascospori hyalini, 1-septati, lato-ovoidei vel lato-ellipsoidei, tegminibus irregularibus, hyalinis, gelatinosis, circumdati.

Perithecia black or dark-brown, carbonaceous, innate, subglobose, ostiolate; paraphyses sparse. Asci broad-cylindric or broad-clavate, deliquescing, 4–8-spored. Ascospores hyaline, 1-septate, broad-ovoid or broad-ellipsoid; each surrounded by an irregular, hyaline, gelatinous sheath.

Didymosamarospora euryhalina sp. nov.

Perithecia nigra vel atro-brunnea, carbonacea, innata, subglobosa; ostiolis papillatis, centricis vel excentricis; 226–336 μ longa ac 328–430 μ per diam., paraphysibus sparsis. Asci lato-cylindricales vel lato-clavati, ad apicem rotundi vel truncati; unitunicati, deliquescentes; sporis 4 usque ad 8; 96–127 x 17–31 μ. Ascospori hyalini, 1-septati, lato-ovoidei vel lato-ellipsoidei, aequilaterales, quaque cellula uniguttulata, ad septum aut leviter aut haud constricti; tegminibus irregularibus, hyalinis, gelatinosis circumdati; 25–34 x 12–17 μ, plerumque 28–30 x 14–16 μ; saepe abortantes.

Perithecia black or dark-brown, carbonaceous, subglobose, usually flattened basally; 226–336 μ high by 328–430 μ in diam.; innate except for the short, broad-papilliform ostiole; occasionally with two ostioles. Paraphyses sparse, apices rounded; simple. Asci broad-cylindric to broad-clavate, apices rounded or narrowly truncate, basal portion narrow; 4–8-spored; thick-walled, becoming thin-walled at maturity; unitunicate, deliquescing; 96–127 x 17–31 μ. Ascospores hyaline, 1-septate, broad-ovoid or broad-ellipsoid, rarely obovoid; ends rounded or broadly tapering; both cells equilateral, rarely inequilateral; each cell with a single, large guttule; each spore surrounded by a hyaline, gelatinous, irregular sheath, rarely by a narrow one; wall not constricted at septum or inconspicuously so; 25–34 x 12–17 μ, predominantly 28–30 x 14–16 μ; frequently aborting.

In culms of *Juncus roemerianus*, Mullet Pond, Shackleford Banks, North Carolina, August 23, 1956 (TYPE), September 29, 1956.

The collection of the type material was made in the west end of Mullet Pond. The host was growing in freshwater, and the culm tissue within which the ascocarps were found was completely submerged. Records of salinity in this portion of the pond show a fluctuation between 0.0‰ and 0.7‰ for 19 months. The second collection was made in the northeastern portion of the inlet to the pond, in the area subject to neap tides. As in the first collection, the portion of the culm in which the ascocarps occurred was completely submerged at low spring tide.

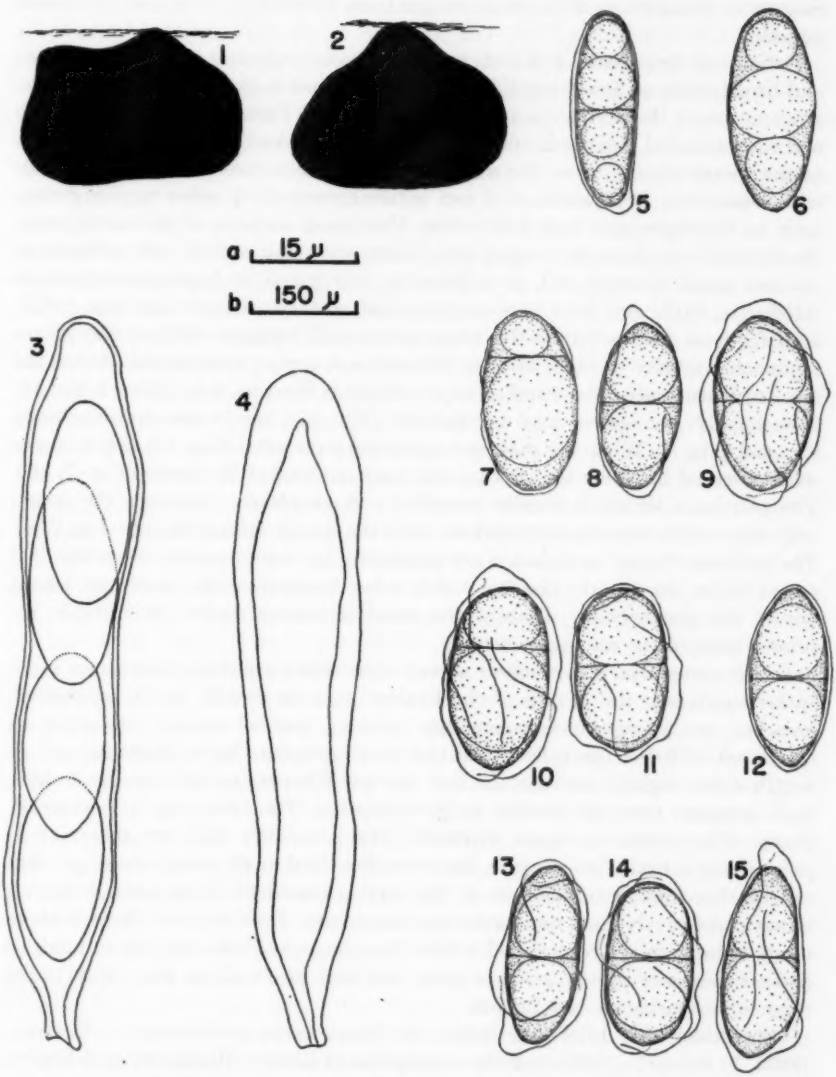

FIG. 1–15. *Didymosamarospora euryhalina*. FIG. 1, 2. Silhouettes of perithecia. FIG. 3. Immature ascus with spore initials. FIG. 4. Immature, thick-walled ascus. FIG. 5. Ascospore with thin sheath; each cell biguttulate. FIG. 6. Immature ascospore. FIG. 7–15. Variations in ascospore shape and gelatinous sheath. Fig. 1, 2, scale b; others, scale a.

Salinity in this portion of the pond ranged from 33.6–35.7‰ over a seven-month period.

Ostioles of the perithecia of *Didymosamarospora euryhalina* are generally short and broad-conic or broad-papilliform. Only the apex is exserted above the substratum, hence the perithecia are easily overlooked. Paraphyses are very sparse and in occasional perithecia, none are in evidence. Asci apparently deliquesce as the spores mature, since the majority of perithecia observed were filled only with ascospores. Deliquescence of asci occurs commonly in other marine genera such as *Ceriosporopsis* and *Lulworthia*. Free-hand sections of immature perithecia, however, show developing asci. These are thick-walled, and without an obvious apical channel such as is found in young asci of *Leptosphaeria acuata* (Hodgetts, 1917) and the marine and brackish water *L. discors* (Johnson, 1957). Judging from the fact that the entire ascus wall becomes thin as the spores approach maturity (that is, with the formation of septa), it is concluded that the asci are unitunicate. The usual ascospore shape is illustrated in figures 9 and 14. Occasionally, the spores may be obovoid (Fig. 15); rarely are they narrowly ellipsoid (Fig. 5). While the septum is generally equatorial (Fig. 12), a few spores were observed in which the septum was near one end of the spore (Fig. 7, 10). The gelatinous sheath is usually irregular, and completely surrounds the spore; only very rarely were spores found on which the sheath was incomplete (Fig. 7, 8). The undulate "wing" or sheath is not persistent. In water mounts, either distilled or sea water, the sheaths dissolve within a few hours after the spores are forced out of the perithecium. None of the usual mounting media are suitable for preservation of the ascospore sheath.

Didymosamarospora euryhalina agrees with *Samarosporella pelagica* in ascospore length and the nature of the hyaline wing or sheath. In *D. euryhalina*, however, the spores are conspicuously broader, and, of course, two-celled as compared with the one-celled condition in *S. pelagica*. Ascus shape as well as length differ slightly between the two species. Whereas paraphyses are lacking in *S. pelagica*, they are present in *D. euryhalina*. The two fungi are evidently nearly alike except for spore septation. The possibility that the spores of *S. pelagica* are actually one-septate, but were described at an immature stage, cannot be dismissed. Examination of the type material of *S. pelagica*, however, shows conclusively that the spores are nonseptate. Furthermore, there is absolutely nothing in the careful and critical descriptions of other species in Linder's paper to indicate that *S. pelagica* alone was described without due regard to the stage of maturity of the fungus.

Other than very brief descriptions of *Samarospora potamogetonis* (Rostrup, 1893a, b; Saccardo, 1895) and the assumption of Linder (Barghoorn and Linder, 1944, p. 407) that *Samarosporella* ". . . appears to be related to *Samarospora* of Rostrup . . .", there is little detailed information on which to base an analytical comparison of *Samarospora* and *Didymosamarospora*. The perithecia of *S. potamogetonis* are olivaceous to brown, superficial, and nonostiolate. The latter feature may or may not be significant. Repeated observations show that some aquatic lignicolous ascomycetes purported to have short-ostiolate perithecia actually

have long ostioles. The short-ostiolate condition often comes about by decomposition and wave or current action. Globose asci are characteristic of *S. potamogetonis*; the asci of *D. euryhalina* are broad-cylindric or clavate. Furthermore, the spores of Rostrup's species are considerably smaller than those of *D. euryhalina*, and, as in *Samarosporella pelagica*, are nonseptate.

Since there are no illustrations of *Samarospora potamogetonis*, the similarity of ascospore appendage (or sheath) among the genera *Samarospora*, *Samarosporella*, and *Didymosamarospora*, may justifiably be questioned. Rostrup described the ascospores of his species as having ". . . einem häutigen, unregelmässig geflügelten Anhängsel. . . " Saccardo termed the appendages "samariform". Linder, on the other hand, characterized the appendages on the spores of his species as ". . . wings which are somewhat undulate and of irregular width. . . ." The "wings" in Linder's figures, however, are unmistakably equivalent to the irregular or undulate sheath on the ascospores of *D. euryhalina*. The winged appendages described by Rostrup, it may be argued, are subject to various interpretations. *Remispora maritima* Linder produces ascospores with gelatinous, hyaline, terminal appendages which are certainly analogous to wings. The same may be said for Höhnk's *Remispora lobata*. The supposed similarity of ascospore appendages of *Samarospora* and *Samarosporella* is open to question; there is some doubt, therefore, that *Didymosamarospora* is identical to *Samarospora* in this feature. The question cannot be solved until Rostrup's species is again collected and studied in the living condition.

In justifying the erection of a new genus for this fungus, the principal issue is the degree of emphasis to be placed on ascospore septation, admitting that in all other characteristics, *Didymosamarospora* is essentially analogous certainly to *Samarosporella*, and quite likely to *Samarospora*. The existing method of grouping many genera of ascomycetes is, perforce, based on obvious characteristics such as spore color and septation. This system of grouping, while not necessarily artificial, is certainly arbitrary, yet is nonetheless of considerable practical significance. The Saccardo system, therefore, while of little phylogenetic importance, perhaps, has the advantage of allowing for ready location of genera or species. Were *D. euryhalina* to be considered a species of *Samarosporella*, the generic concept of the latter would, perforce, be emended to include species with two-celled spores (Didymosporae) and species with one-celled spores (Amerosporae). Adoption of such a procedure would be incongruous in view of the fact that convenience rather than natural relationships apparently establishes the position of ascomycetous taxa within generic or familial boundaries. It seems in order, therefore, to establish a new genus, until such time as a less arbitrary system of generic separation is devised and adopted generally.

SUMMARY

Didymosamarospora euryhalina is described as a new genus and species of Ascomycetes. It is compared with *Samarospora potamogetonis* Rostrup and *Samarosporella pelagica* Linder, but is separable at the generic and specific levels on the basis of ascospore septation.

ACKNOWLEDGMENTS

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TWO NEW CHYTRIDS IN PURE CULTURE, *PHLYCTOCHYTRIUM PUNCTATUM* AND *PHLYCTOCHYTRIUM IRREGULARE*

BY WILLIAM J. KOCH[1]

Department of Botany, University of North Carolina, Chapel Hill, North Carolina

The two species described in this paper were found in United States and New Guinea soils baited with pollen and boiled leaves. Pure cultures were made of them, and all observations recorded are of these single spore cultures either on agar or on natural substrata. These species are interesting because they point up certain difficulties in the use of the apophysis, sporangium development and shape, operculation, vesicular discharge, zoospore, and relationship of the thallus to its substratum, as taxonomic criteria. These features are discussed after the diagnoses of the species.

Since monocentric chytrids are relatively difficult to purify, some details of the methods used for getting single spore cultures are noteworthy. As a matter of expediency the same media used for maintaining stock cultures and for study purposes are used in the original isolations. These are *PDP*, made by adding 50 mg. peptone, 9 gm. dextrose, and 9 gm. agar to 900 ml. of potato juice, which is made by boiling 150 gm. diced potato tubers in a liter of water for one hour and straining the resulting soup through a cloth towel; *K-1*, which contains 0.6 gm.

[1] The author is grateful to Dr. J. N. Couch for encouraging help and criticism and to Dr. E. K. Goldie-Smith and Dr. A. I. Suskin for writing the Latin descriptions.

peptone, 0.4 gm. yeast extract, 1.8 gm. glucose, and 9.0 gm. agar added to 900 ml. water; and *YpSs* of Emerson, 1941.

If the chytrid is too sparse for obtaining enough zoospores in relation to the number of bacteria and other contaminants in the original collection, either an enrichment culture or a unifungal culture must be made. However, if the chytrid is sufficiently abundant, the material on which it is growing is transferred to a drop or two of sterile distilled water on a glass slide. Zoospore discharge is thus stimulated and the drop of water in which the liberated zoospores are swimming is transferred with a capillary pipette to the surface of an agar medium in a petri dish, near one edge. Instead of streaking the spore suspension in the traditional manner with a wire loop, Dr. M. B. Huneycutt and the author have worked out a more satisfactory method for separating the chytrid zoospores from contaminants. The petri dish is tilted so as to cause the drop to run out, forming a line of spore suspension across the plate. A few drops of sterile distilled water are added to this line at the position of the original drop and the petri dish is again tilted, but this time at right angles to the line of suspended spores. The result is that the spores are dispersed in a comb-shaped film of water on the agar surface. Next, the petri dish is propped in a nearly vertical position. The surface of the agar is then allowed to dry, for about five or ten minutes, and the petri dish is then covered and set aside for incubation. After the bacterial colonies have become just large enough to detect under a high power dissecting microscope, single chytrid germlings, free from bacteria and other contaminating organisms, are removed with a very small spatula which has been cut from flattened "chromel" wire, and transferred to a fresh agar plate. If contamination is not too great a problem, it is desirable to wait until the chytrid thalli have matured, insuring the transfer of viable thalli.

Sometimes too few sporangia liberate their zoospores at one time to make the above method feasible. In such a case one can remove from the substratum, placed on an agar plate, one or several large, mature sporangia, push them around by means of a finely sharpened needle on and within the agar in order to remove most of the contaminants, and transfer these sporangia to a small drop of water, where zoospore discharge will occur (Couch, 1939). Then it is possible to proceed as outlined above.

In the subculturing of certain monocentric chytrids, once a pure culture has been established, approximately one ml. of sterile distilled water is poured onto the inoculum in a fresh culture plate, flask or tube. The water covers a large part of the agar surface in a petri dish and consequently zoospores from the inoculum can spread out over a large area. This increases by many times the amount of growth in a single petri dish, and sometimes it is the only method by which a species can be transferred satisfactorily, as in the second species described in this paper.

Phlyctochytrium punctatum sp. n. (Fig. 1–12)

Sporangium sessile vel interbioticum; globosum (6–47μ in diam.) vel elongatum; leve aut setigerum; 1–15 parvis papillis emissariis; membrana hyalina vel rufa-fulva, multis punctis minutissimis. Systema rhizoideum ramosum, parva

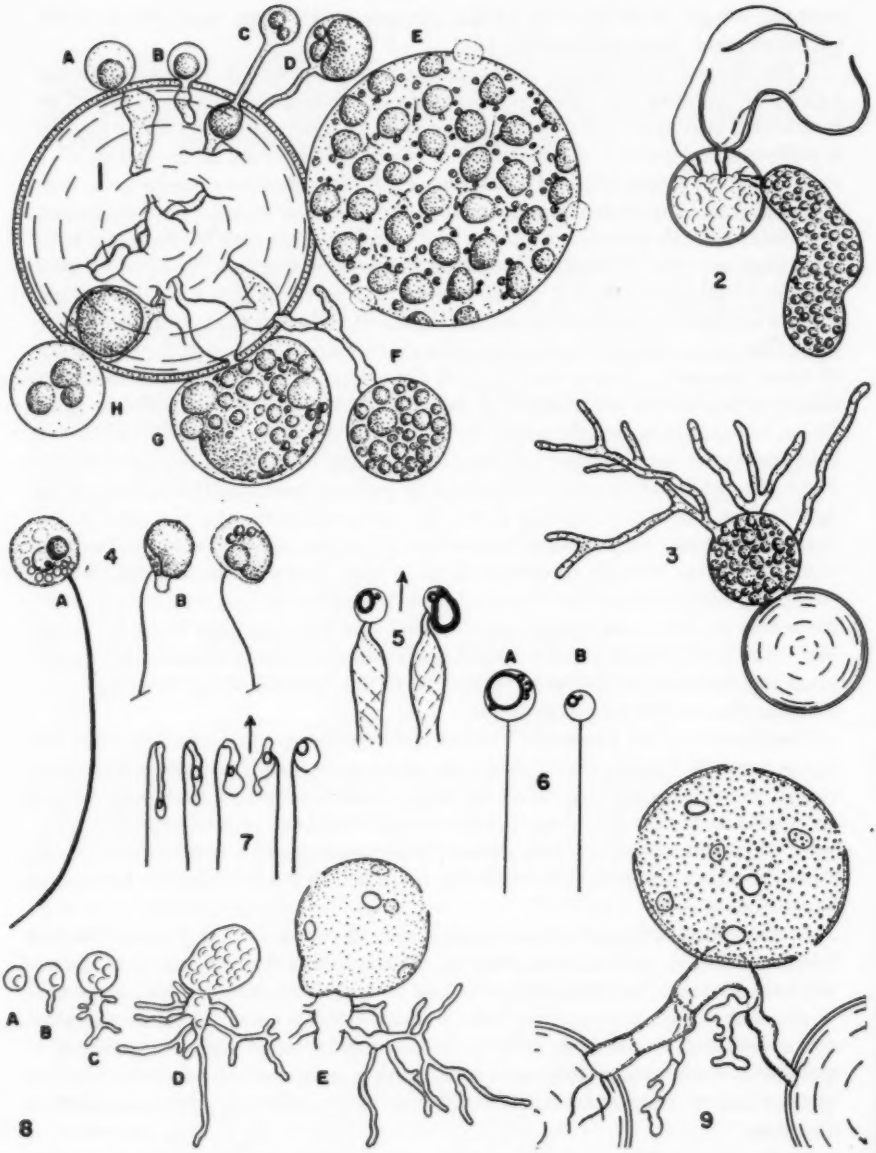

FIG. 1–9. *Phlyctochytrium punctatum*. FIG. 1. Composite figure showing camera lucida drawings of 8 thalli of "C-CH" on one diagrammatically represented pollen grain of sweet gum. ×1350. FIG. 2. Three thalli of "Lucas" that have self-parasitized the chytrid sporangium in *K-1* agar culture. ×850. FIG. 3. Zoosporangium of "La6b" with sporangial hairs;

apophysi. Zoospora globosa (2.6–6.1μ in diam.) vel elongata; singulis vel pluribus globis oleis; flagello 18.4–24.5μ longo, varie ad subbasem vel ad apicem adfixo. Spora perdurans non visa.

Sporangium sessile, stalked, or rarely interbiotic; smooth or rarely with 1–6 rhizoid-like, simple or branched hairs up to 75μ long and 2.5μ wide; spherical or subspherical, at times obpyriform or elongate on agar culture media; 6–47μ in diam.; with 1–15 inconspicuous discharge papillae, each 0.8–5.0μ in diam., consisting of a palely glistening plug, not covered with a wall, protruding 0.5–5.0μ; with a wall up to 1μ thick, remaining intact after zoospore discharge, colorless to rusty brown, smooth, with numerous minute punctations or pits up to 0.5μ in diam. Rhizoidal system with a spherical, subspherical or elongate and irregularly expanded apophysis, up to 9μ across when spherical, or at times without an apophysis on agar culture media; with a relatively sparce system of broad, blunt rhizoids branched at right angles. Zoospores emerging slowly and singly after deliquescence of the papillae; spherical, subspherical, irregularly elongate or rod-shaped when swimming; 2.6–6.1μ in diam. when spherical; characteristically with one conspicuous eccentric and subapical lipoid body, often with several other smaller ones, the conspicuous lipoid body small to large, often nearly filling the spore body; with a posteriorly directed whip-lash flagellum 20.5 (18.4–24.5)μ long, subbasally, laterally, subapically or apically attached. Resting spore not seen.

Named for the numerous punctations seen on empty sporangial walls.

On *Liquidambar styraciflua* and *Pinus taeda* pollen and *Paspalum dilatatum* leaves used as bait in soils from New Guinea (TYPE), Louisiana, North Carolina, and Michigan. On the resting spores of *Peronospora tabacina*, North Carolina. Type cultures have been sent to the American Type Culture Collection, Washington, D. C., and to the Centraalbureau voor Schimmelcultures, Baarn, Netherlands.

The diagnosis and other observations are based on the following single spore isolates, all of which were brought into pure culture: "NG-3", found and brought into pure culture by J. N. Couch from soil sent by Lane Barksdale from New Guinea in 1944. "La6b", isolated in April, 1953, on sweet gum pollen and boiled paspalum leaf bait from sandy soil by a marsh near New Orleans, La. "C-CH", collected in May, 1953, on pollen bait from soil below the strawberry patch in J. N. Couch's garden, Chapel Hill, N. C. "Lucas", growing on the resting spores of *Peronospora tabacina* in tobacco plant beds near Whiteville, Columbus Co.,

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pollen grain diagrammatic. ×600. FIG. 4A. Zoospore of "La6b" from *K-1* agar culture after staining vitally with janus green B and then fixing with osmic acid. Note nucleus (in optical section), extranuclear granules and lipoid body. ×2100. FIG. 4B. Living zoospores of "Lucas" momentarily at rest, from pollen culture. ×2100. FIG. 5. Diagrams of zoospores of "Lucas" from pollen culture, swimming in water, showing body shapes and positions of attachment of flagellum. Observed with 60× darkfield lens. FIG. 6. Diagrams of typical zoospores of "Lucas" from pollen culture (A) and from *K-1* agar (B). FIG. 7. Diagrams showing shapes of zoospores of "La6b" swimming on surface of agar media. FIG. 8. Development of a zoosporangial thallus of "NG-3" on *YpSs* agar. Note irregular expansion of old zoospore cyst. A. 1:00 p.m., 7 Nov. '56. B. After 9 hrs. C. After 21 hrs. D. After 29 hrs. E. After 45 hrs. and after zoospore discharge. ×600. FIG. 9. Empty interbiotic thallus of "C-CH" with rhizoids penetrating 2 diagrammatically represented pollen grains and with 10 discharge pores and numerous pits in the sporangium wall. ×850.

North Carolina, was found by G. B. Lucas and L. H. Person of North Carolina State College and brought to this laboratory for identification and culture in April, 1955 (see Person, Lucas, and Koch, 1955).

A single germ tube, which is the initial rhizoid, grows from the encysted zoospore (Fig. 1B, 8B). Although the pattern of development which follows is also typical for *Phlyctochytrium*, there is evidence from sequential observations of individual thalli that in some cases a portion of the germ tube may expand and become part of the zoosporangium. This has not been determined with certainty but is indicated in the type material growing on *YpSs* agar.

The rhizoidal system of *Phlyctochytrium punctatum* is difficult to see within pollen or leaf tissue, but it shows up clearly on interbiotic thalli or on thalli in pure culture on agar. The rhizoids are relatively sparse, stout, blunt and untapered or with a rather uniform width except near the sporangium, and they branch at right angles (Fig. 10, 11). This contrasts with the species which follows (Fig. 13, 14), although rhizoidal systems with multiple axes, as in figure 14, are also found in *P. punctatum*.

An apophysis can usually be seen on thalli growing on natural substrata (Fig. 1). The apophysis results from the swelling of the base of the young rhizoidal axis (Fig. 1A, C; 8D), and as it enlarges the crotch and the base of one or more branch-rhizoids may be incorporated, often resulting in a lobed, flattened or otherwise irregular apophysis (Fig. 1F). Thalli have been seen on pollen with extramatrical and intramatrical apophyses resembling Rosen's (1887) figures 15 and 17 for *Phlyctochytrium zygnematis*. A distinct apophysis may form on a thallus growing in pure culture on agar media, as seen in figure 10, but it is usually less distinct or lacking (Fig. 11). No distinct apophysis is seen on self-parasitic thalli (Fig. 2).

There is a characteristic early stage of development when the apophysis is nearly completely filled with one lipoid body (Fig. 1C, H). Subsequently this large lipoid body breaks up into smaller ones which pass into the developing sporangium. The enlarging sporangium has many relatively big lipoid bodies of variable size, often with one much larger than the rest. It is convenient to refer to this as the *accumulation stage* of sporangial development (Fig. 1D, G). The large lipoid bodies break up into a great many more small ones of rather uniform size. This has been called the *granular stage* of development (Fig. 2, 3). The tiny lipoid bodies then coalesce, one large and often one or more smaller ones being located in each zoospore initial. Cleavage of the protoplast into zoospores probably occurs during the granular stage and mature discharge papillae have been seen on sporangia in this stage.

That the physical relationship between the chytrid and its substratum may be quite variable is especially clear when it is growing on sweet gum pollen. Typically the rhizoidal system is completely endobiotic and the epibiotic sporangium is sessile (Fig. 1B, G; 2; 3). On the other hand, part of the germ tube is often epibiotic (Fig. 1C, D), resulting in a mature thallus with a stalked sporangium. Figure 1F shows a young thallus with a rhizoidal system external to the substratum and beginning to branch. Mature thalli have been seen with much-

branched rhizoidal systems external to the substratum (Fig. 9) and with the tips of the rhizoids of a single thallus entering as many as three pollen grains. Often, in such a case, some of the rhizoids fail to contact the substratum. Such interbiotic thalli are occasionally found in pollen cultures in distilled water but are rare or lacking in those in soil water, where the rhizoidal system in nearly every case is completely endobiotic and the sporangium is epibiotic and sessile. This

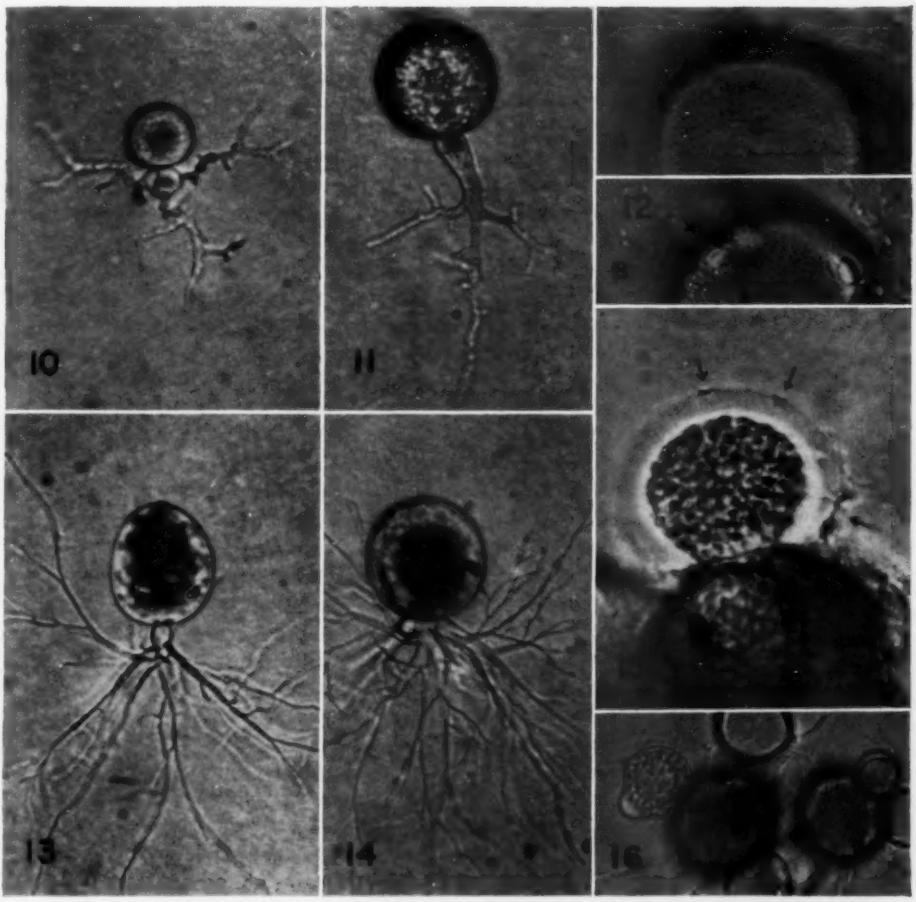

FIG. 10–12. *Phlyctochytrium punctatum*, isolate "Lucas." FIG. 10, 11. Young thalli growing on *K-1* agar. ×600. FIG. 12. Surface views of portions of two sporangia from pollen cultures showing punctations on wall. Arrows indicate discharge pores. ×1200. FIG. 13–16. *Phlyctochytrium irregulare*. FIG. 13, 14. Young thalli growing on *K-1* agar. ×120. FIG. 15. Sporangium about 10 sec. after initiation of zoospore discharge. Arrows indicate fragments of papilla wall. ×800. FIG. 16. Two pollen grains with one mature sporangium (left), 3 empty sporangia, and a mature resting spore (right). ×515.

variation in thallus-substratum relationship exists, but to a lesser degree, for the other species described in this paper, and has been observed in other genera which would not normally be classified as interbiotic. This range of variation is interesting particularly in view of the fact that the interbiotic thallus is a feature of the family Rhizidiaceae and not of the Phlyctidiaceae, in which *Phlyctochytrium* belongs (see Sparrow, 1943).

Figs. 8E, 9 and 12 show the punctations or pits of empty sporangial walls, seen with a 60× oil immersion objective. The color and punctations of the sporangium wall may vary with culture conditions. Sporangia growing on *Paspalum* leaf tissue in distilled water are light rusty brown. The walls of empty sporangia are usually colorless and the punctations are not seen or are frequently indistinct in thalli on sweet gum pollen on the surface of distilled water. However, on pine pollen the walls of empty sporangia are colorless or pale tan to rusty brown and the punctations tend to be more distinct. The punctations and pigmentation are enhanced by the addition of boiled dead oak leaves to the water or by the use of soil water. In mass growth on *K-1* agar, after one week, "La6b" is colorless while "Lucas" is slightly pigmented (Cream-buff in Ridgway, 1912).

Many of the sporangia of "La6b" growing on pollen floating on soil water produce 1–6 coarse, rhizoid-like hairs (Fig. 3) which extend out as much as 75 microns from the surface of the sporangium. Sporangial hairs are occasionally formed in pollen cultures in distilled water, but they were overlooked until a special search was made for them. They may be simple or as much as thrice branched. Like the rhizoids (Fig. 10, 11), the sporangial hairs are blunt and with a rather uniform width. Their appearance suggests that they may have an irregularly spiral pattern of growth. The hairs on developing sporangia contain clear cytoplasm and many relatively large vacuoles. Sporangial hairs have not been noted in the other isolates.

In pure culture on agar "Lucas" may parasitize itself; then the sporangia are usually elongate and irregular, up to five times longer than broad at maturity (Fig. 2). The rhizoidal system of a self-parasitic thallus is either slightly branched or simply a short, unbranched, tapering tube. The fact that the fungus can parasitize itself is indeed a remarkable phenomenon, and the fact that the sporangium of a parasitic thallus has a special shape is perhaps even more remarkable, especially since such a difference in sporangial shape is usually taken as an indication of specific difference in the Chytridiales. However, that *Phlyctochytrium punctatum* has the genetic capacity for this extreme variation in shape is observed in "NG-3" growing saprobically on *YpSs* agar, where young sporangia may be subovoid or obpyriform, although most sporangia are apparently spherical throughout their development. Young sporangia that are obpyriform have been followed to maturity, and those observed remained obpyriform, with the narrower basal part small and inconspicuous and with the distal part large and nearly circular in outline, so that the mature sporangium for the most part appeared spherical. Young sporangia that are subovoid (Fig. 8D) are at maturity essentially spherical except for a hump near the base (Fig. 8E). The developmental sequence followed in figure 8 shows that at first the old zoospore cyst expands evenly (A–C), and that later just a portion continues to expand (D, E).

There is no evidence of a nuclear cap in living zoospores or in zoospores that have been stained with crystal violet or janus green B and observed in wet mounts. On the other hand, these stains are taken up by a number of granules which are clumped toward the base of the zoospore body and more or less surround the nucleus (Fig. 4A).

In water, zoospores are spherical, subspherical, or irregularly elongate as they swim (Fig. 4B, 5). In a thin liquid film on the surface of agar some of the zoospores are subspherical, most are irregularly elongate, and many are even thinly rod-shaped (Fig. 7). This is an expression of greater amoeboid activity on agar and is a phenomenon described by Gaertner (1954a) for his species of *Phlyctochytrium*.

There are two conspicuous differences between the zoospores of "Lucas" from pollen and those from *K-1* agar (Fig. 6). First, the zoospores are larger when they come from pollen cultures. Spherical zoospores measure 5.5 (3.6–6.1)μ from pollen and 3.7 (2.6–4.8)μ from agar. Second, from pollen cultures the zoospores have more lipoidal material—a greater number of lipoid bodies and also a larger conspicuous one. There are 2–11 lipoid bodies per zoospore when from pollen cultures and 0–6 when from agar cultures. In pollen cultures the conspicuous lipoid body is 4.3 (1.8–5.1)μ in diameter whereas from agar it is 1.0 (0.3–1.7)μ. In contrast, flagellar length is apparently constant—19.7 (16.9–21.4)μ in pollen and 19.5 (18.4–21.4)μ in agar cultures.

Also noteworthy is the fact that the zoospores from "Lucas" and "La6b" growing on pollen differ enough to indicate that they may represent different taxa. "Lucas" differs consistently from "La6b" in that in the former the flagellum is shorter, the whip-lash tip of the flagellum is longer, the zoospore body is larger, there are more lipoid bodies per zoospore, and the conspicuous lipoid body is larger *per se* and in relation to spore body size. These are features which can be subjectively observed and substantiated by measurements, although the two isolates do overlap.

One of the most interesting features of *Phlyctochytrium punctatum* is that the posteriorly directed flagellum is apical, subapical, lateral or subbasal but apparently never truly posterior in attachment. The flagellum is subbasal on spherical or subspherical zoospores (Fig. 5, left), lateral or subapical on irregularly elongate zoospores (Fig. 7; 5, right), and apical only on the thinly rod-shaped zoospores (Fig. 7). Gaertner (1954a) observed apical flagella on the elongate zoospores of his species of *Phlyctochytrium*. Only with the 60× darkfield lens has the slight, but important, distinction between basal and subbasal attachment been detected. Here the point of attachment of the active flagellum is seen by noting the position on the spore body of the base of the double image (Fig. 5). The double image is the visual image of the rapidly undulating flagellum (Couch, 1941). With the brightfield or phase contrast microscope such zoospores (Fig. 5, left) appear to have flagella truly or completely posterior, which is actually the case in the subsequently described species (Fig. 24).

Phlyctochytrium punctatum resembles *P. synchytrii* Köhler, parasitic on the resting sporangia of *Synchytrium endobioticum*; *Phlyctochytrium lippsii* Lohman (1942), which parasitizes the ascospores of *Ascobolus* spp., *Lasiobolus equinus* and

Sordaria coronifera; and *Phlyctochytrium spectabile* Uebelmesser (1956), growing on pine pollen. However, *Phlyctochytrium punctatum* differs from these species in having a sporangium wall that is densely covered with minute punctations or pits, at times pigmented, and at times with rhizoid-like hairs. Also, there may be more discharge papillae and the apophysis is not as conspicuous as in *P. synchytrii*. The discharge papillae of *P. punctatum* are not elevated from the main contour of the sporangium wall as indicated by Lohman's figures for *P. lippsii* and by Reinboldt (1951) for an unnamed species growing on pine pollen, and the discharge plugs are not as long (not "finger-like") as in *P. synchytrii*. *Phlyctochytrium punctatum* also somewhat resembles *P. palustre*, *P. africanum* and *P. kniepii* described by Gaertner (1954b), but it differs from Gaertner's species probably as much as his three species differ from each other or from *P. synchytrii* and *P. lippsii*, and in none is the sporangium wall pitted, pigmented, or with sporangial hairs. *Phlyctochytrium punctatum* on agar is seen to have a characteristic rhizoidal system (Fig. 10, 11), in which the rhizoids are relatively sparce, blunt and with a rather uniform width, branched at right angles, and with a variable apophysis or none. This is for the most part like the rhizoidal systems of the three species of Gaertner (1954b; fig. 1e–i, 2a, 4c & d, 6e). *Phlyctochytrium punctatum* is quickly identified by the many, fine punctations visible on empty sporangial walls.

Phlyctochytrium irregulare sp. n. (Fig. 13–24)

Systema rhizoideum ramosum, parva apophysi. Sporangium sessile vel interbioticum; globosum (8–58μ in diam.) vel ovoideum; membrana hyalina vel rufa-fulva, multis punctis indistinctis; 1–2 magnis papillis emissariis. Emissio zoosporarum plerumque per vesiculum, aliquando per operculum cardinatum. Zoospora globosa, 2.6–4.6μ in diam.; pileo parvo nucleari et singulo globo olei eccentrico; flagello 16.8–23.5μ longo, postice fixo. Spora perdurans subrufa-fulva, modo sporangii lata; globosa.

Rhizoidal system consisting of branched, tapered rhizoids, usually with a spherical, subspherical or elongate and irregularly expanded apophysis which is 3.2–12.2μ across when spherical (usually 3.5–6.5μ) or often without an apophysis on agar culture media. Sporangium sessile, stalked, or rarely interbiotic; spherical, subspherical, elliptical or ovoid; 8–58μ in diam. when spherical; with a dark to light reddish-brown or colorless wall, up to 1.5μ thick, remaining intact after zoospore discharge, and with numerous barely visible punctate markings; with one or sometimes two subbasal, lateral, subapical, or rarely apparently apical discharge papillae that are broad, hemispherical or truncate, 3–14μ wide and 3–9μ high, and that contain a palely glistening plug substance; after zoospore discharge with rim of pore often recurved and either rough or smooth. Zoospore discharge occasionally with the formation of a flap-like or hinged lid, the wall of the discharge papilla, but usually inoperculate. First zoospores emerging in a motionless mass surrounded by a zone of the expanding plug substance, which often is bordered either with a vesicle, that is the expanding papilla wall, or with several fragments of the papilla wall; dispersing rapidly after dilution of the surrounding plug substance and after rupture of the vesicle when present. Zoospores remaining in sporangium swarming and emerging one or two at a time. Zoospore spherical or subspherical; 3.7 (2.6–4.6)μ in diam.; with a palely glistening, irregular or lobed nuclear cap; with an eccentric, subapical to mid-lateral

lipoid body which is small or sometimes fills over half the zoospore body; with whiplash flagellum, 21.7 (16.8–23.5)μ long, posteriorly attached and directed. Resting spore light reddish-brown; borne like the sporangium; spherical; 14.6μ in diam.; nearly filled with a large lipoid body.

Named for the variation in method of zoospore discharge.

On *Liquidambar styraciflua* pollen and *Paspalum dilatatum* leaves used as bait in wet soils from North Carolina (TYPE) and Michigan.

Phlyctochytrium irregulare is described from one collection made in February, 1955, from wet soil in the greenhouse of the Coker Arboretum at the University of North Carolina, Chapel Hill. It was brought into pure culture on *PDP* and *K-1* agar media at that time. The diagnosis and other observations are based on a single-spore isolate. This species was also found in Smith's bog, Cheboygan Co., Michigan, in July, 1956.

The resting spore seen in figure 16 is the only one that has been found. That it is a resting spore of this chytrid is almost certain because the pollen culture in which it was found was made by inoculating with thalli from pure culture. Its color is like that of the sporangium, and its shape and huge lipoid body indicate that it is probably a true resting spore and not simply a dormant zoosporangium.

The zoosporangial phase of *Phlyctochytrium irregulare* resembles that of *P. hallii* Couch (1932), a parasite of *Spirogyra*, with respect to sporangium shape, zoospore discharge in a mass from a relatively large pore, and its branched rhizoidal system with an apophysis which, although less variable in shape, is also sometimes lacking. Sizes of the sporangium, apophysis, and zoospore are also approximately similar.

In the development of the zoosporangial thallus a single germ tube grows out from the encysted zoospore (Fig. 17c) and branches to form a rhizoidal system. The rhizoids differ in several ways from those of *Phlyctochytrium punctatum* (cf. fig. 10 and 13). The rhizoidal system in *P. irregulare* is relatively more copious; the rhizoids are longer and thinner, appearing more delicate, they taper more, and they branch at acute angles.

On pollen the apophysis has the same morphological variation (Fig. 17d, f, h; 22) as in *Phlyctochytrium punctatum*, although the apophysis is less distinct. Also as in *P. punctatum* there is a characteristic early stage of development on pollen when the apophysis is filled with one lipoid body (Fig. 17a, b) which subsequently breaks up into smaller ones (Fig. 17g) that pass into the developing sporangium. On agar a recognizable apophysis is usually lacking and is represented by no more than the large rhizoidal base or bases under the sporangium (Fig. 13, 14, 19). These two species lead one to question the presence or absence of an apophysis alone as a tenable generic criterion for the separation of *Phlyctochytrium* and *Rhizophidium*.

While the rhizoidal system is developing, the zoospore cyst enlarges to form the zoosporangium. The same changes in lipoidal content of the developing sporangium of *Phlyctochytrium punctatum* occur in *P. irregulare*. In these species the lipoidal material extends to the periphery of the sporangium (Fig. 1G, 17b).

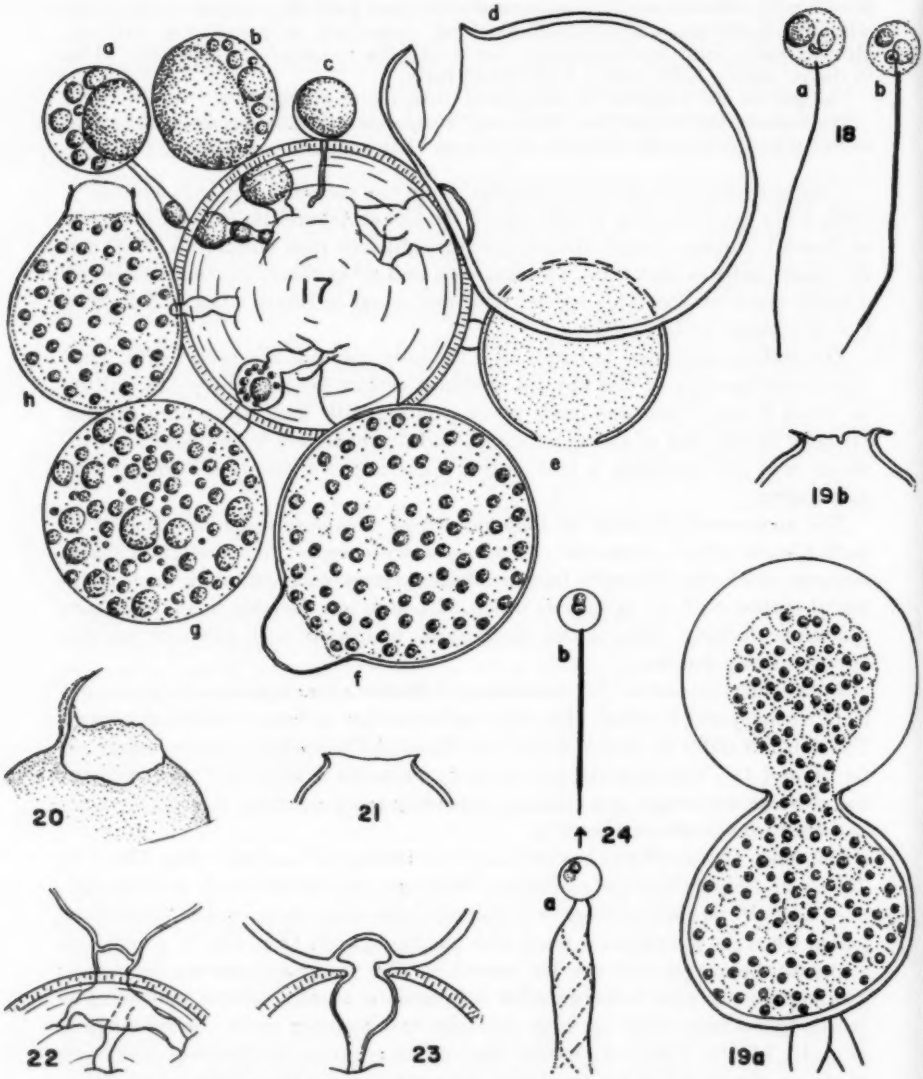

FIG. 17–24. *Phlyctochytrium irregulare*. FIG. 17. Composite figure showing camera lucida drawings of 8 thalli on one diagrammatically represented pollen grain. ×1350. FIG. 18. Zoospores, from pollen culture. a. Living, momentarily at rest, showing lipoid body and lobed nuclear cap. b. After staining vitally with janus green B and then fixing with osmic acid, showing nucleus and rhizoplast as well as lipoid body and nuclear cap. ×2100. FIG. 19. a. Sporangium about 10 sec. after initiation of zoospore discharge, showing vesicle which ruptured a few seconds after this drawing was made. b. Pore of same sporangium after all

This differs, for example, from *Chytridium sexuale* where in the accumulation stage the lipoid bodies are centrally clustered, leaving an irregular margin of cytoplasm (Koch, 1951).

A mature sporangium, which may be larger on agar culture media (up to 146μ in diam.) than on sweet gum pollen (up to 58μ), is cut off from its rhizoidal system by an arched cross wall. The cross wall may be right at the bases of the sporangium and rhizoidal system (Fig. 17h) or it may be raised slightly on the side wall of the sporangium (Fig. 22, 23). When growing on pollen in the original collection, the sporangium wall is reddish-brown. In subsequent cultures on pollen in distilled water the color is paler or often apparently lacking. On pollen in distilled water to which boiled, dead oak leaves have been added, the original reddish-brown color is restored. Macroscopically the culture in mass growth is greenish on *K-1* agar (Ecru-olive in Ridgway, 1912) and light brown on *PDP* agar (Buckthorn Brown in Ridgway, 1912). In water mounts of thalli on pollen the very minute punctate markings (Fig. 17e) show up better with the 35× oil immersion lens than with the 40× dry or 90× oil lenses. They are clearly visible on all large, empty sporangia when carefully looked for; otherwise they are overlooked. The large and conspicuous discharge papilla with its palely glistening plug has been seen fully formed as early as the granular stage of sporangial development. Its size is correlated approximately with the size of the sporangium producing it. The greenhouse isolate growing on pollen has one papilla per sporangium, while on agar there are frequently two papillae. This may be correlated with the larger sporangial size on agar; however, two papillae per sporangium were often found on the Michigan collection growing on pollen.

The most interesting feature of this species is its variation in method of zoospore discharge: 1. Usually, the papilla wall, which is actually the sporangium wall that surrounds the discharge plug, becomes irregularly thinned (Fig. 17f) or, when this is not apparent, at least develops places of relative weakness. When the zoospores begin to emerge, surrounded by a zone of the viscous plug material (Fig. 15, 19a), the thin papilla wall expands. If it continues to expand, the emerging spores are surrounded by the expanding and thinning plug substance which is bordered by the thinning papilla wall or vesicle with a thicker part or parts often clearly seen (Fig. 19a). This stretching wall or vesicle is not elastic enough to contain the entire spore complement and ruptures before the emerged spores start to swim away. The rupturing vesicle, which may otherwise be invisible, can often be located by the bacteria and minute pieces of trash which adhere to it. 2. If the papilla wall ruptures when the spores begin to emerge from the sporangium, no vesicle is formed. In this case one of two things may happen: First, the thickened part or parts of the ruptured papilla wall may be carried out on

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spores have left. ×850. FIG. 20. Pore of empty sporangium showing "operculum". Surface view. ×1350. FIG. 21. Pore of empty sporangium showing smooth, recurved rim. Optical section. ×1350. FIG. 22, 23. Bases of empty rhizoidal systems and sporangia, showing cross walls. ×1350. FIG. 24. Diagrams of a zoospore observed with 60× darkfield lens. a. Spore body oscillating and flagellum undulating perpendicularly to line of observation. b. Spore body rotated 90°.

the periphery of the expanding plug substance—as many as eight or ten fragments have been seen. Second, if the rupture is incomplete and at the base of the papilla, the papilla wall is pushed back, forming a hinged lid or operculum (Fig. 17d, 20). Both situations may obtain on the discharge of a single sporangium, as in figure 15, where wall fragments are indicated with the two upper arrows and a partial "operculum" by the arrow to the right. 3. In some cases most or all of the papilla wall dissolves completely before discharge (Fig. 17h) so that there are no papilla wall fragments, vesicle or operculum formed on the discharging sporangium. Whatever the particular method of discharge is, the first zoospores emerge in a motionless mass and disperse rapidly after sufficient dilution of the surrounding plug material. The zoospores remaining in the sporangium swarm and emerge one or two at a time. The pore of the empty sporangium in rare cases is smooth and not raised from the main contour of the sporangium (Fig. 17e), but more frequently the pore has a raised, recurved lip with a rough margin (Fig. 19b, 21).

The formation of a discharge vesicle has been reported in *Phlyctochytrium zygnematis* (Rosen) Schroeter by Rosen (1887), in *P. planicorne* Atkinson by Sparrow (1932 and 1938), and in *P. chaetiferum* Karling (1937), in which it could not be determined whether the vesicle is a surface tension membrane or a morphological membrane. In the latter two species the zoospores may also emerge singly through the discharge pore. In *P. unispinum* Paterson (1956) the zoospores are liberated upon dissolution of the vesicle into which they were discharged. The vesicle here is plug material and not wall. Also, in a species of a closely related genus, *Rhizophidium sphaerocarpum* (Zopf) Fischer, the zoospores emerge in a delicate evanescent vesicle derived from the inner sporangial wall (Zopf, 1884). It is clear that the *vesicle* may have different meanings for different species. In some cases it originates from the sporangium wall and in others from the discharge plug. This needs to be studied further before vesicular discharge in different taxa can be compared.

Willoughby (1956) finds that occasionally in *Rhizidium richmondense* Willoughby a portion of the sporangial wall may separate as a lid-like structure, but he still regards this chytrid as essentially inoperculate. A similar situation is described for *Rhizophidium vaucheriae* de Wildeman (1931). Sparrow (1943) notes that zoospore discharge in *R. vaucheriae* "is evidently similar to that found in *Blastocladia pringsheimii* (Sparrow, 1932, 291) where a cap is often observed for a short time at the apex of the mass of emerging zoospores but more often dissolves completely before the swarmers are discharged." It is possible that the hinged papilla cap which is occasionally formed at zoospore discharge in *Phlyctochytrium irregulare* can be interpreted as an expression of true operculation. The hinged or incompletely formed operculum does occur in truly operculate genera; the author found it frequently in *Chytridium sexuale* and also regularly in three undescribed species of *Chytridium*. Nevertheless, *Phlyctochytrium irregulare* is at least predominantly inoperculate, and at the present time a more incisive interpretation cannot properly be made. It emphasizes the need for a definitive study of operculation and inoperculation.

In the living zoospore (Fig. 18a) the tilted nuclear cap is the most conspicuous structure, aside from the glistening lipoid body. After staining, the nucleus and rhizoplast can be seen (Fig. 18b).

Under experimental conditions it was found that size and shape of the zoospore body, flagellar length, and position of attachment of the flagellum were the same whether the zoospores came from thalli growing on pollen or on *K-1* agar culture medium. However, under the same conditions there were striking differences in the lipoidal material. From pollen there are fewer lipoid bodies per zoospore (0–3 compared with 0–5), a greater number of zoospores have just one lipoid body (92 per cent compared with 64 per cent), and the conspicuous lipoid body is larger [2.3 (1.0–3.3)μ compared with 0.6 (0.2–1.8)μ]. A similar situation exists with regard to the lipoidal content in *Phlyctochytrium punctatum*, isolate "La6b". However, in isolate "Lucas" of *P. punctatum* (Fig. 6), although the conspicuous lipoid body is also larger on pollen, there are more lipoid bodies per zoospore and none of the zoospores have just one lipoid body. These data indicate that in zoospores the lipoidal content is especially subject to variation, and this suggests that special caution should be exercised in the taxonomic use of the lipoidal content of chytrid zoospores.

SUMMARY

The morphology and development of two new species of *Phlyctochytrium* are described from single-spore isolates growing on natural substrata and on agar culture media. *Phlyctochytrium punctatum* sp. n. is especially characterized by a globose, multiporous, punctate or pitted sporangium wall, which may be pigmented and with several branched sporangial hairs, and by a characteristic rhizoidal system with a highly variable apophysis. *Phlyctochytrium irregulare* sp. n. is chiefly characterized by its large, eccentric discharge papilla, its unusual methods of zoospore discharge, its pigmented and finely punctate sporangium wall, and by a characteristic rhizoidal system with a highly variable apophysis. These species are interesting because they point up certain difficulties in the use of the apophysis, sporangium development and shape, operculation, vesicular discharge, zoospore, and relationship of the thallus to its substratum, as taxonomic criteria. Pure culture techniques are described.

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NORTH AMERICAN LEJEUNEACEAE
VI. LEJEUNEA: INTRODUCTION AND KEYS; SUBGENUS LEJEUNEA (I)

BY RUDOLF M. SCHUSTER

Department of Botany and University Herbarium, University of Michigan, Ann Arbor, Michigan

Lejeunea, in North America, is almost exclusively restricted to the southeast, with all but five species occurring in Florida. The species not extending into the tropics and subtropics, however, occur in the Appalachian Mountains. As a consequence, every species of the genus found in North America can be found in the southeast.

The genus *Lejeunea* is here used in a broader sense, equivalent to the usage in Schiffner (1893), than is customarily the case today. As accepted here, it includes the two "genera" *Stylolejeunea* Sim, as delimited by Evans (1940), and *Microlejeunea* (Spruce) Evans. The reasons for such a conservative generic treatment are subsequently outlined in detail.

There has been but a single revision of the North American species of *Lejeunea*, that of Evans (1902). In this paper eight species are treated that are now referable to *Lejeunea*. Evans (1905, 1917, 1918) added a number of other species to the area treated, and carefully treated the involved synonymy of several species. The data given by Evans were compiled in the work of Frye and Clark (1947), with the unfortunate introduction of a misleading key, and of a number of serious errors regarding the synonymy of the species, and of their limits. Recent studies, dealing with specific aspects of the Lejeuneaceae, have been very helpful in making possible a modern revision of the genus. Among these are the admirable paper by Evans (1935) on stem-anatomy; that by Schuster and Hattori (1954) on cytology; and the papers by Buch (1934) and Greig-Smith (1954) dealing with several species. In the present revision sixteen species and three additional varieties are regarded as well-established members of our flora. Twelve of these taxa belonging to the subgenus *Lejeunea* and three extraterritorial taxa are treated in the present part of this revision; the remainder will be dealt with in the next part of this series.

The present study of the genus is the first based on personal knowledge of the various species *as living organisms*. All but one of the species have been repeatedly collected personally, and studied while living, during the last twelve years. It deserves emphasis that in extremely complex and difficult groups, of which *Lejeunea* is one, our species concepts must be based on as diverse a series of concepts as possible. The distinctive distribution patterns, the diagnostic cytological features, and often characteristic ecological restrictions can be studied only on the basis of extensive personal field work. These factors have been scarcely dealt with in North America, with the consequence that the systematics of the genus have been in some respects unsatisfactory. This has been reflected in the high incidence of erroneous range extensions published in recent years, such as the extension of *L. cavifolia* to Mississippi and Florida (Frye and Clark, 1947), the extension of *L. serpyllifolia* to the outer Piedmont of the southeast (Frye and Clark, 1947), the report of *L. patens* from the continental portion of North America, in western Ontario (Cain and Fulford, 1948).

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wife, Olga M. Schuster, both in conjunction with the field work pursued during the course of this investigation, and in connection with the preparation of this paper. Dr. Doris Raymond has kindly prepared the Latin diagnoses.

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LEJEUNEA LIBERT[1]

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Eulejeunea Schiffner, *in* Engler-Prantl, Nat. Pfl.-Fam. **1**(3): 122, 1895; Stephani, Sp. Hep. **5**: 701, 1914.[2]
Eulejeunea subgenus *Microlejeunea* Schiffner, *in* Engler-Prantl, Nat. Pfl.-Fam. **1**(3): 124, 1895.
Eulejeunea subgenus *Archetypica* Massal., Jubul. Fl. Ital. 6, 1912.
Stylolejeunea Evans (1940; not of Sim, 1926).

Plants minute to medium-sized, *pale green* or *yellowish-green to pure green*, usually in mats or patches, decumbent, more or less closely adnate. Leafy shoots quite flat, mostly 200–1500μ wide. Stems essentially prostrate, slender, formed of 7 rows of cortical cells and 3–14 or more rows of medullary cells, which are (more or less) thin-walled and slightly to conspicuously smaller than the cortical cells; stems nearly uniform, the branches essentially like main axes, microphyllous branches absent. Rhizoids frequent, originating from a small number of rhizoid-initials (rarely a larger number, forming a discrete, if small, disk). Leaves distant, approximate, or distinctly if not densely imbricate, flat or slightly, rarely strongly, convex, their position when dry and when moist essentially the same, spreading narrowly to widely laterally in a nearly flat plane. *Lobules extremely variable*, ranging from uniformly obsolete (reduced to 1–2-celled vestiges), then sometimes with filiform, elongate apical teeth, to small but inflated, to extremely large and approaching the lobes in surface-area; lobules, except when reduced to vestiges, with *hyaline papilla at proximal base of the 1-celled apical tooth;* apical tooth small and obtuse to slightly elongated, *never tapering and acuminate.* Cells either uniform (*Lejeunea*) or sometimes dimorphic and with a few ocelli (*Microlejeunea*), with colorless walls, not collenchymatous or weakly so, rarely with slightly bulging trigones and discrete intermediate thickenings, often with walls slightly and nearly equally thickened, convex but never developed as conical tubercles; oil-bodies varying from very numerous (30–50 per cell), and minute and homogeneous, to several per cell (2–10) and finely segmented or papillose in appearance, rarely 1–2 per cell and formed of rather fine segments, *never exceedingly large and obscuring the lumen* (the leaf-cells thus always char-

[1] Originally spelled *Lejeunia* by Libert. However, for the last 75 years the emended spelling *Lejeunea* has been almost universally accepted; it is retained here.

[2] Stephani describes the genus as *Eulejeunea*, but on all the succeeding pages lists the species under *Lejeunea*.

acteristically pellucid or subpellucid). Underleaves *moderate or small in size*, 1–3.5 times as broad as stem, distant to slightly imbricate, *never prominently cordate or auriculate, bilobed for 0.35–0.65 of their length*, the lobes erect, *never strongly divergent*, entire or rarely with a lateral tooth or angulation near base. *Asexual reproduction quite absent.*[3]

Dioecious or autoecious. Male inflorescences very polymorphic (often within the same species), either on short lateral leafless branches and then terminal, or on elongate leafy shoots, then usually becoming intercalary by subsequent vegetative growth; bracts saccate, subequally bilobed, usually somewhat shorter than vegetative leaves (often strongly reduced in size when on abbreviated leafless lateral branches); usually diandrous; bracteoles present at base of androecial spike only (most species) or present throughout (*L. laetevirens*). Female inflorescence exceedingly diverse in position, either terminal on a leading branch (then almost invariably innovating from one side, becoming pseudolateral; rarely innovating from both sides, becoming situated in an apical bifurcation), or often terminal on a very short lateral branch (then invariably with a single innovation); *innovations almost always again fertile*, often within 2–3 pairs of leaves, the inflorescences then frequently situated along one side of a superficially unbranched, elongated axis. Bracts bilobed, the lobule varying from very large to vestigial; bracteole shallowly to deeply bilobed, *often united at base with one or both bracts*. Perianth *not to distinctly dorsiventrally compressed, 5-carinate* on distal 0.3–0.7, the *carinae sharp but entire* (at best slightly crenulate from projecting cells), *not produced* as horns or auricles (rarely extended upward to level of apex of beak as low, rounded auricles).

TYPE: *Lejeunea cavifolia*, a common species of cool and temperate regions of Europe and eastern North America.

As is evident from the cited synonymy, the writer regards *Microlejeunea* as generically inseparable from *Lejeunea* s. str. In support of this position may be cited the fact that there is no difference whatsoever in form of the perianth, of the male or female bracts, of the oil-bodies or cell-walls, in shape and form of the lobule, or form of the underleaves which can be used to effect a separation into two genera. *Microlejeunea*, as the name implies, includes merely the more highly reduced species. Implicit is also greater delicacy and, consequent upon reduction, a tendency towards a simpler stem anatomy. If one compares the stem-anatomy of such "typical" species of "*Eulejeunea*" as *L. flava* (Fig. XXVI: 6), one finds that the seven rows of cortical cells surround as many as 10–14 rows of smaller medullary cells, while such species of *Microlejeunea* as *bullata* and *laetevirens* exhibit only three rows of medullary cells within the seven cortical cell-rows. However, studies of a series of species show total intergradation in stem-anatomy. For instance, Evans (1935) illustrates the stem of *Lejeunea* (*i.e.* "*Eulejeunea*") *inundata* Spr., a South American species. This, as in the reduced species of *Microlejeunea*, has only three rows of medullary cells.

The most recent attempt to maintain the two groups as generically distinct is that of Vanden Berghen (1948). In his key this author separates the two taxa only on the basis of size ("filiform" vs. "more robust") and on the basis of the

[3] Müller (1916, p. 660) and Frye and Clark (1947) report it as present and by discoid, multicellular gemmae. In no bona-fide species of the genus, even as broadly conceived as it is here, is such a mode of reproduction known. It must be kept in mind that, at one time, all the Lejeuneaceae were placed in the portmanteau genus *Lejeunea*, including such types as *Cyclolejeunea*, *Diplasiolejeunea* and *Cololejeunea*, which freely produce discoid gemmae. To the writer's knowledge, no species, which is correctly retained within the genus, possesses either "gemmae" or caducous leaves.

relatively large size of the lobule, as compared with the lobe in *Microlejeunea* versus the "more reduced" lobule of *Lejeunea* s. str. No other differential characters of any validity can be found in the author's diagnoses of these two taxa. Evans (1902, 441, 443) was one of the first to accept *Microlejeunea* as a genus. In his generic diagnoses, the only differences between the two groups given are those of comparative size, difference in direction of the lobes of the leaves, and a fancied difference in leaf-cells (those of *Lejeunea* being supposedly thin-walled, those of *Microlejeunea* thick-walled).

A careful study of the various species assigned to *Microlejeunea* shows that none of these distinctions is constant. For instance, *M. laetevirens* and *M. cardoti* have relatively small lobules and widely spreading leaves; the same is true, to a lesser degree, of *M. ruthii*. Indeed, of the five species of the genus occurring in our area, only two (*M. ulicina* and *M. bullata*) would key to the genus in the work of Vanden Berghen. The impossibility of maintaining any distinction is also evident from the key in Frye and Clark, where *Microlejeunea* and *Lejeunea* jointly appear ten times in the key to genera given to the schizostipous groups! This difficulty in assigning well-marked limits to the two taxa is also evident from a study of the European species. *Lejeunea diversiloba* is regarded by Macvicar (1926) and Buch (1934) as a species of *Lejeunea* s. str., while Spruce (1884, p. 287) and Greig-Smith (1954) place it in *Microlejeunea*.

In the final analysis, *Microlejeunea* differs from *Lejeunea* s. str. only in the following *tendencies*, none of which affords a sharp separation of the taxon: (1) reduction in area of lobe, with consequently greater comparative size of the lobule; (2) less widely spreading leaves; (3) a weak tendency for the development of ocelli in a few species; (4) a weak tendency for the development of smaller cells, which are more or less equally thick-walled; (5) a reduction of the stem to the point where only three medullary cell rows are retained. These are regarded as insufficient for the retention of a generic separation, and the writer consequently follows the excellent example of Schiffner (1895) in considering the two as subgenera of a single genus.

To these two subgenera it appears advisable to add *Stylolejeunea* (sensu Evans, 1940; nec Sim, 1926) as a third subgenus. It will be developed subsequently that *Stylolejeunea* in the original sense of Sim, i.e., as to the genotype, must be regarded as a simple synonym of *Rectolejeunea*. Study of authentic material of both *S. duncanii* and *S. rhodesiae* reveals that they possess caducous leaves. Therefore the two American species assigned by Evans (1940) to "*Stylolejeunea*" need reinvestigation. These two species, *L. pililoba* and *L. spiniloba*, have the persistent leaves characteristic of *Lejeunea* s. str. They differ from *Lejeunea* s. str. largely in the vestigial lobuli with attenuated, filiform apical teeth, and in the compressed perianth. A similar but less constantly developed, and less attenuated, apical tooth is found in *Stylolejeunea* sensu Sim and in phases of several species currently assigned to *Rectolejeunea*.

The writer is of the opinion that the development of a strongly attenuate and elaborated apical tooth of the lobule cannot, by itself, serve as an adequate generic character. The species of *Lejeunea* s. str. with reduced lobules often bear

elongate apical teeth 2–3 cells long. From this, the derivation of the *Stylolejeunea*-like lobule is easily possible. The polymorphism described by Arnell (1953) for the lobule of *Stylolejeunea* (or *Rectolejeunea*) *rhodesiae* throws serious doubt upon the value of this character. The only other "generic" character assigned to *Stylolejeunea* is a compressed perianth, with the dorsal keel reduced. However, *L. longifissa* and other species of *Lejeunea* show perianths which exhibit compression to a greater or lesser degree (Fig. XLII: 2–3). For these reasons, *Stylolejeunea* in the sense of Sim (= *Rectolejeunea* Evans) and "*Stylolejeunea*" Evans (nec Sim) hardly represent well developed genera. For "*Stylolejeunea*" sensu Evans, nec Sim, including *L. pililoba* and *L. spiniloba* the new subgeneric name *Chaetolejeunea* is proposed. This subgenus is based on the reduced lobule with highly elaborated apical tooth, and on the compressed form of the perianth.

It is suggested that the interested student compare fertile plants (or the plates of these here given) of *Lejeunea longifissa* St. and "*Stylolejeunea*" *pililoba* (Spr.) Evs. The overwhelming similarity between the two was impressed on the writer in a specimen from Puerto Rico (Bayamon, *A. A. Heller 147*, NYBG), where the two species occurred admixed, together with *L. minutiloba* Evs. The perianths of the two species are extraordinarily similar, showing an obovate-obcordate outline in both cases, with a low dorsal keel distally, sharp, wing-like lateral keels and less sharp, but quite discrete postical keels (Fig. XLII: 1–3, 7–9). Suggestively similar are also the deeply bifid underleaves, in both cases with more or less divaricate, lanceolate lobes. Indeed, the only "generic" difference is that of the lobule. In view of the extraordinary polymorphism of the lobule in *Lejeunea* s. str., it seems unwarranted to found a genus on such a character. The superficially very different lobule of *Stylolejeunea* represents a mere elaboration of the terminal cells of the vestigial lobules of such species as *L. minutiloba* and *L. cladogyna*. It was furthermore shown by Schuster and Hattori (1954) that the oil-bodies of *Stylolejeunea* showed no major differences from those of most species of *Lejeunea*.

In this connection, the distressingly close affinity of *Rectolejeunea* Evs. to *Lejeunea* Libert must be brought up. The traditional difference cited between the two genera (as in Vanden Berghen, 1948, p. 14) is based on the "distinctement comprimé" perianth of *Rectolejeunea*, versus the "non comprimé" perianth of *Lejeunea*. On this basis, such species as *L. longifissa* key clearly to *Rectolejeunea*. Indeed, there appears to be nothing to separate the perianths of *Rectolejeunea phyllobola* from those of *Lejeunea longifissa*. *Rectolejeunea*, like *Lejeunea*, shows extraordinary polymorphism, as regards the lobules, and (as was shown by Schuster and Hattori, 1954) has oil-bodies that are similar to those of some species of *Lejeunea*. Yet the situation with respect to the generic separation of *Lejeunea* and *Rectolejeunea* is more complex, and less easily resolved, than that with respect to *Lejeunea* and *Stylolejeunea*. *Rectolejeunea* includes dull plants, tending to develop characteristically small but equally thick-walled cells, which are densely chlorophyllose (with the consequence that the plants are more opaque). Furthermore, nearly all bona fide species of *Rectolejeunea* appear to show asexual reproduction by means of caducous leaves. This feature is absent in all true species of

Lejeunea known to the writer. In fact, we would regard this as the major generic criterion affecting a separation of *Rectolejeunea* from *Lejeunea*, in spite of the fact that this peculiarity in *Rectolejeunea* is mentioned nowhere by Vanden Berghen (1948).[4] For the time being, therefore, *Rectolejeunea* is kept separate from *Lejeunea* s. str. Pertinent to this is the fact that although the least specialized species of *Rectolejeunea* (of which *R. phyllobola* is an excellent example) are nearly inseparable from *Lejeunea*, except on the basis of development of a mode of asexual reproduction, the more specialized species develop a number of peculiarities (such as scattered ocelli; type of oil-bodies; exceedingly small and thick-walled cells; highly derivative and specialized caducous leaves, etc.) that place them far above any true species of *Lejeunea* in respect to their level of specialization. Because of this, the writer (in Schuster and Hattori, 1954) suggested that the genus *Rectolejeunea* be split into two subgenera, of which the less derivative is perhaps more clearly allied to *Lejeunea* s. str. than to the more specialized subgenus. This problem merits further attention.

Finally, the extremely close relationship between *Lejeunea* and *Crossotolejeunea* must be admitted. "Typical" species of *Crossotolejeunea* differ from *Lejeunea* s. str. in two important features: (a) the perianth-keels are laciniate or dentate; (b) the leaves are acute or apiculate. With the peripheral species of *Crossotolejeunea*, such as *C. bermudiana* Evs., these distinctions may virtually disappear. In *C. bermudiana* the perianth keels are armed with two rows of crenulate-protuberant cells, rarely developed as two-celled teeth. Such keels can be almost matched in *Lejeunea patens* and other species of *Lejeunea*, where the two rows of cells bordering the keels are strongly inflated or even slightly dentiform-produced. In such unspecialized species of *Crossotolejeunea* as *C. bermudiana*, the

[4] The entire problem of the distinctness of *Rectolejeunea* from *Lejeunea* is complicated to a large extent by two exotic species, "*Stylolejeunea duncanii*" Sim and *Microlejeunea rotundistipula* var. *pallida*" Hattori (Jour. Hattori Bot. Lab. **5**: 53, fig. 36a–c, 1951) = "*Lejeunea pallida*" Hattori (*ibid.* **8**: 36, 1952), the former South African, the latter Japanese. The first species is the type of *Stylolejeunea*, but is not particularly close to *Stylolejeunea* sensu Evans (1940). It has, *teste* Arnell and E. J. Jones (*ad lit.*) caducous leaves, and according to Arnell is probably identical with "*Stylolejeunea*" *rhodesiae* Sim. *If* caducous leaves occur in the African species, this, together with the compressed perianth would place them in *Rectolejeunea*! In that case, *Stylolejeunea* becomes a synonym of *Rectolejeunea*, a course which is the more probable because Arnell (1953) has already placed *S. rhodesiae* into *Rectolejeunea*, admitting its "intermediate" position to *Stylolejeunea*! The two species, which, following Evans (1940) American bryologists have put into *Stylolejeunea*, will have to be given a new generic (or subgeneric) name.

Lejeunea pallida of Hattori shows equally distressing features. It lacks caducous leaves—at least in the specimens available to me—but has the strongly compressed, obcordate perianth typical of *Rectolejeunea*. Also, it shows the sharp tendency for the underleaves to produce weak lateral angulations or teeth that characterize most species of that genus, and has the somewhat hexagonal, thick-walled, non-collenchymatous cells with occasional lenticular intermediate thickenings that are commonly found in *Rectolejeunea*. All in all, I believe that, in spite of the absence of caducous leaves, it must be placed in *Rectolejeunea* as *R. pallida* (Hattori) comb. n. This, however, compels us to admit that the ultimate criterion which we have relied on for the discrimination of *Rectolejeunea*, i.e., the ability to form caducous leaves, is also only an inconstant criterion!

leaves, although typically crenulate, may be rounded evenly at the apices, except on juvenile shoots. Like *Rectolejeunea*, *Crossotolejeunea* represents a relatively major evolutionary branch, and is perhaps validly retained as a distinct genus.

In addition to the close affinities to the taxa which have been mentioned above (*Microlejeunea*, "*Stylolejeunea*", which are reduced to subgeneric standing; *Rectolejeunea* and *Crossotolejeunea*, which I am reluctantly compelled, for the time being, to leave as "good" genera), *Lejeunea* shows distressingly close affinities to several other so-called genera. Three of these are *Taxilejeunea*, *Potamolejeunea*, and *Hygrolejeunea*. It is perhaps not wholly fortuitous that of these genera, *Microlejeunea*, *Taxilejeunea*, *Lejeunea* and *Potamolejeunea* all include species with minute, homogeneous oil-bodies; all but the last show variation from this to species with rather finely segmented, moderately sized oil-bodies.[5] The rest of these taxa, i.e. "*Stylolejeunea*", *Crossotolejeunea* and *Rectolejeunea* have only compound oil-bodies, as far as known, and the latter two "tend" to have them larger and with coarser segments than is typical of the remainder of the complex of genera and subgenera enumerated. However, there are no such sharp differences between genera in oil-body form as Schuster and Hattori (1954) demonstrated for the genera of Holostipae. Indeed, the only marked difference in oil-body form, compound vs. simple and homogeneous, is intrageneric, being found in *Microlejeunea*, *Lejeunea*, and *Taxilejeunea*, and perhaps elsewhere.

As we have seen previously, the "genera" *Stylolejeunea*, *Microlejeunea*, *Crossotolejeunea* and *Rectolejeunea* differed from *Lejeunea* in such palpable morphological features as lobule size and form, and perianth form (specifically, number of keels and whether they were armed or smooth). However, no such clearly morphological differences exist to separate *Taxilejeunea*, *Potamolejeunea*, *Hygrolejeunea* and *Lejeunea*. The following conspectus perhaps expresses the more obvious differences, which are admittedly inconstant:

a. Gynoecia with innovations, which are (in at least some cases) again fertile..... b.
b. Gynoecia numerous, either cladogynous (with the innovations typically repeatedly fertile, forming serially oriented, cymose systems) or if acrogynous often or usually with 2 innovations; usually robust plants with underleaves very large, usually cordate to auriculate at base, inserted by an arched line; underleaves typically contiguous to quite overlapping; cells usually with large trigones and intermediate thickenings. (With usually one or more evidences of specialization such as: subentire underleaves; perianth keels toothed, or vestigial; beak absent; leaf-lobes often acute and sometimes toothed)..... c.
c. Gynoecia typically all, or largely, cladogynous; the cladogynous gynoecia with single innovations that are typically repeatedly fertile, forming serially oriented, closely juxtaposed, cymosely oriented systems; gemminate innovations absent or only sporadic; underleaves usually bifid or at least retuse..... d.

[5] Greig-Smith (1953, 1954) discusses the oil-bodies of "*Microlejeunea diversiloba*" and *Potamolejeunea holtii*, which have "simple" oil-bodies; Schuster and Hattori (1954) have shown a wide variation in oil-body form in *Lejeunea* s.str., and I have found (unpublished) that in *Taxilejeunea* we have species both with segmented or compound oil-bodies, and with minute, homogeneous oil-bodies.

d. Without asexual modes of reproduction; leaves rounded to acute at apex; underleaves usually large and contiguous, usually rounded to cordate at base; perianth keels smooth to absent to lamellate, not usually spinose to laciniate ..... *Taxilejeunea*

d. With thallus-like brood-bodies from the margins of the lobes: leaves drawn out and shortly acuminate at apex; underleaves remote, small, cuneate to narrowly rounded at base; perianth keels dentate to spinose-dentate ..... *Stenolejeunea* gen. n.[6]

c. Gynoecia typically acrogynous, at least in part, and then with 2 innovations which may again be fertile, never with serially oriented lateral gynoecial systems; plants large but delicate, with large and imbricate, cordate to auriculate underleaves that are bilobed or entire; leaves usually convex, with deflexed apices.. *Hygrolejeunea*

b. Gynoecia always partly cladogynous (the cladogynous inflorescences with single innovations, which remain sterile, or occasionally produce a single inflorescence), partly acrogynous (the acrogynous inflorescences usually with single innovations, rarely with 2); usually delicate plants, with small, remote to barely contiguous, bifid underleaves that are narrowed or cuneate or narrowly rounded at base, usually as long as or longer than broad, inserted nearly transversely; cells usually leptodermous, with small or no trigones, only rarely with discrete intermediate thickenings. (Without any of the aforementioned evidences of specialization) ..... *Lejeunea*

a. Gynoecia without innovations, all cladogynous and on very short lateral branches; otherwise like *Lejeunea* ..... *Potamolejeunea*

Eifrig (1937) has already adequately demonstrated the patent impossibility of sharply separating *Taxilejeunea* from *Hygrolejeunea*; indeed, he implies that future work may well show that the schizostipous *Hygrolejeuneae* can be divided down between *Lejeunea* and *Taxilejeunea*. Eifrig also stated that *Lejeunea* grades into *Taxilejeunea* through *L. flava*, and I would consider that various other species he cites, particularly in the Taxilejeuneae quinquecarinatae, are also clearly transitional. This intergradation, particularly in orientation of the gynoecia, is discussed in more detail under *Lejeunea flava*. I, for one, question the wisdom of maintaining a generic distinction here.

Greig-Smith (1948) briefly discusses *Potamolejeunea*, and brings out the traditional distinction from *Lejeunea*, namely the presence of "elongate stems pinnulate with nearly sessile female branches, the latter simple or with one small, normally sterile innovation." *Lejeunea* s. str. is supposedly different in that its species "have more irregularly arranged, often long, female branches with one or more innovations which are sometimes fertile." Schiffner (1893), who can hardly be accused of being a taxonomic conservative, either in genus or species concept, was unwilling to accept *Potamolejeunea*, although he accepted almost all of Spruce's other novelties. Evans also clearly did not regard *Potamolejeunea* as of any generic value, since his *Lejeunea cladogyna*, which he described as with the

[6] Type, *Taxilejeunea thallophora* Eifrig (Ann. Bryol. **9**: 99, fig. XII, 1, 1937); containing, in addition, *S. apiculata* (Sande-Lac.) comb. n. I consider the presence of a specialized mode of reproduction, together with the thoroughly specialized morphological features, warrants placing these two species in a separate genus. In no other species in the entire complex of genera to which I have alluded in the preceding discussion, except in *Rectolejeunea* species, do we find any mode of asexual propagation. In *Rectolejeunea* we find caducous leaves.

gynoecia wholly on short lateral branches with short and sterile innovations, would fall into *Potamolejeunea*; this is clear from Fig. XLVIII: 10. The lack of faith in *Potamolejeunea*, as a genus, is even clearer from the treatment accorded *Lejeunea patagonica* Steph. and *L. corralensis* Evs., two Chilean species treated by Evans (1930). *L. patagonica* and *L. corralensis* agree very closely, as Evans points out, both possessing wholly cladogynous inflorescences on short lateral branches; in *L. patagonica* there are no innovations whatsoever, in *L. corralensis* the gynoecia each possess a short and sterile innovation! Except for this difference, as Evans emphasizes, the species differ only in slight characteristics. Both species, using the criteria relied on by Greig-Smith, would go into *Potamolejeunea*, as would *Lejeunea cladogyna*. However, as I demonstrate under this last species, *L. cladogyna* shows perfect transition to the more typical Lejeuneae in the following respects: although usually cladogynous with short and sterile innovations, as in *L. corralensis*, occasional innovations are elongate and leafy; and, although almost always cladogynous, isolated acrogynous inflorescences have been found! *Lejeunea glaucescens*, which Evans describes as constantly cladogynous, is similarly variable, although here we find that the cladogynous inflorescences not infrequently bear fertile innovations (Fig. XXXV: 1), while occasional acrogynous innovations occur. Even *Lejeunea holtii*, which Greig-Smith would place in *Potamolejeunea*, is admitted by Macvicar (1926) and Evans (1930), to be variable insofar as it usually lacks innovations, but occasionally produces short sterile ones! I therefore am convinced that *if Potamolejeunea* is separated from *Lejeunea* merely on the basis of the position of gynoecia and absence of innovations, it cannot be maintained. The situation is more complex, however, since the subaquatic species assigned by Spruce and Stephani to *Potamolejeunea* at least in part show a complex stem anatomy, quite different from that of the vast majority of the Schizostipae (see Evans, 1935). *P. orinocensis* Steph. and its relatively robust affiliated species, all of which possess numerous rows of cortical cells, do not appear closely allied to *Lejeunea holtii*, or to other species of *Lejeunea*.

From the preceding outline one could arrange these species, as well as several others selected to complete this series, as follows:

a. Gynoecia all cladogynous and on very short branches, uniformly lacking innovations. *L. patagonica* Steph., *teste* Evans (1930).

b. Gynoecia all cladogynous and on short branches, usually without innovations, rarely with a short sterile one. *L. holtii* Spr.

c. Gynoecia all cladogynous, but the branches slightly varying in length, all with a single innovation which remains sterile. *L. corralensis* Evs. (*teste* Evans, 1930).

d. Gynoecia almost all cladogynous, the branches almost always very short, with a single usually very short (rarely elongate) and sterile innovation; very rarely with isolated acrogynous inflorescences, sporadically produced. *L. cladogyna* Evs.

e. Gynoecia almost always cladogynous, the branches short, with a short or long innovation which may again be fertile (Fig. XXXV: 1), and in addition with occasional to infrequent acrogynous inflorescences which always have single innovations. *L. glaucescens* and its varieties (p. 137). Showing slight intergradation to the *Taxilejeunea* condition!

f. Acrogynous gynoecia rare or absent; cladogynous gynoecia with 1 innovation that is

again fertile, or remains sterile, but does not produce gynoecia in series. *Taxilejeunea stephanii* Eifrig (= *Hygrolejeunea nymannii* Steph.; see Eifrig, 1937, p. 90, Fig. VI, 1).[7]

g. Gynoecia indiscriminately produced on elongate leading shoots (then with 1, rarely 2 innovations), and on short lateral shoots or elongate leafy lateral shoots; lateral gynoecia with 1 innovation or rarely 2, if with 1 this often again fertile. *L. flava* (Sw.) Nees; see discussion on p. 154 of this paper and in Eifrig (1937). A clear transition to *Taxilejeunea*!

h. Initial gynoecia terminal on leading leafy shoots, with usually 2 innovations and then situated in fork of dichotomy, or with 1 innovation and becoming pseudolateral; also with occasional (rarely none!) to frequent cladogynous inflorescences, which produce a single innovation which is usually again 1–2 times fertile! *L. lamacerina* subsp. *gemminata* Schust. (p. 180). Showing clear transition to the *Hygrolejeunea* condition in the gemminate innovations, to the *Taxilejeunea* condition in the lateral inflorescences with fertile innovations! There is little or nothing to separate this type of orientation of the gynoecia from that in *Taxilejeunea splendida* Eifrig (see Eifrig, 1937, Fig. V).

The preceding series could be documented much more fully, if it were desirable. Such a series shows, however, that: (a) There is such a gradual gradation from the *Potamolejeunea* type of gynoecial orientation to that of *Lejeunea*, that a generic distinction is pointless. I would be willing to accept a subgeneric status for *Potamolejeunea*, and, in such a case, would be inclined to place *L. cladogyna* in this subgenus. (b) Tendencies occur towards production of the gemminate innovations characteristic of most undoubted species of *Hygrolejeunea*; these are present in *L. flava* and *L. lamacerina*. (c) Total intergradation occurs from the supposedly "irregularly arranged" gynoecia of *Lejeunea* to the supposedly regularly cymosely arranged, cladogynous gynoecia of *Taxilejeunea*.

The level of intergradation is so great that I am convinced that we shall have to reduce the so-called genera in this group even further, and perhaps consider the five genera which were separated by the conspectus given above as subgenera only. Certainly the two additional taxa, *Microlejeunea* and *Stylolejeunea* (*sensu* Evans) can hardly be recognized as distinct genera, and these are here formally reduced to the status of subgenera of *Lejeunea*.

The three subgenera of *Lejeunea* that are found regionally, as circumscribed here, may be separated by the following key. Keys to species are given under the individual subgenera.

KEY TO SUBGENERA OF LEJEUNEA

1. Lobules various in form, usually some inflated and large, however constituted never with an apical tooth more than 2–3 cells long; perianth terete or slightly compressed, the dorsal keel well-developed ..... 2.
2. Plants medium-sized (600–1600μ wide in our region), usually autoecious, often with perianths; leaves widely (50–80°) spreading; lobules varying from obsolete to inflated, never more than 0.25× the area of the lobes, not more than 0.4–5× the length of the lobes; ocelli never developed; cells without any marked tendency to develop equally thickened walls; stems with usually 8–12 rows of medullary cells, or more

Subgenus *Lejeunea*

[7] The situation here is exceedingly close to that in *Lejeunea glaucescens*! It is perhaps noteworthy that the plants reported from Tennessee as *L. glaucescens* (Sharp, 1939) represent a species of *Taxilejeunea* which, using illustrations alone, is almost inseparable from *T. stephanii*! A more eloquent demonstration of the validity of the "generic distinctions" between *Lejeunea* and *Taxilejeunea* is hardly necessary!

2. Plants small, often filiform (200–550μ wide), dioecious (in our region), usually sterile, virtually never with perianths; leaves spreading less widely (10–45°), smaller, at most 300μ long; lobules usually large and inflated, at least in part (their area mostly 0.3–0.8× that of lobe; their length 0.4–0.9× that of lobe); ocelli often developed at leaf-bases; cells showing a tendency for the development of evenly thick walls; stems with only 3 rows of medullary cells.....Subgenus *Microlejeunea*

1. Lobules reduced to a small basal fold, bearing a long, linear to narrowly lanceolate apical tooth or appendage, 1–3 cells wide and 5–12 cells long; perianth strongly compressed, the dorsal keel low or obsolete, short; autoecious; otherwise as in *Lejeunea*
Subgenus *Chaetolejeunea* (=*Stylolejeunea* sensu Evans)

Subgenus LEJEUNEA Libert

Lejeunea subgenus *Eulejeunea* Spruce, Trans. Proc. Bot. Soc. Edinburgh **15**: 79 and 260, 1884 (in largest part).

Eulejeunea subgenus *Eulejeunea* s. str. Schiffn. *in* Engler-Prantl, Nat. Pfl.-Fam. **1**(3): 122, 1895.

Eulejeunea subgenus *Architypica* Massal., Jubul. Fl. Ital. 6, 1912.

Lejeunea, sensu Evans (1902), Vanden Berghen (1948), Müller (1916), Frye and Clark (1947), *as genus.*

Plants largely *medium-sized* (650–1500μ wide), with the *leaves widely spreading* (usually 45–80°), usually contiguous to imbricate. *Stems with usually 8–15 rows of medullary cells*, rarely reduced to 3 rows of medullary cells. Leaves with lobules polymorphic in many species, varying from a minute vestigial flap, bearing an apical tooth commonly formed by 1–2 cells, to inflated (then rarely exceeding 0.45× the length of the lobe; *usually less than 0.25× the area of the lobe*); *apical tooth never elaborated to form a linear, elongated appendage.* Cells uniform, the marginal usually 15–24μ, *without ocelli*; walls thin and varying from uniformly leptodermous to slightly collenchymatous, the trigones small to rarely medium-sized and bulging; occasionally with scattered intermediate thickenings.

Usually autoecious (in all of our species) and very abundantly fertile; almost invariably developing perianths. Gynoecia various in position, *some invariably on short lateral branches.* Perianth 5-keeled, *little or not compressed.* Androecia with bracteoles usually only at base.

The subgenus *Eulejeunea* is one of the largest (189 species in Stephani, 1915) and most difficult within the family. Herzog (1952, p. 102) has stated this well: "Die Gattung *Eu-Lejeunea* wird, so lange sie nicht monographisch durchgearbeitet ist, immer ein "crux et scandalum" der Lebermoossystematik bleiben. Hier ist noch die schwierigste Arbeit zu tun." Eifrig (1937, p. 110) refers to it as "die noch ganz ungeklärte Gattung." The chaotic status of the taxonomy of the group is evident from the fact that since the time of Stephani no student has had the courage to describe more than one or two species in the group. Not even Herzog, who has dominated research on the Lejeuneaceae during the last three decades, has described a single species within *Lejeunea*, s. str. Only Stephani had the courage to cope with the group extensively, although he lacked the judgment needed to cope with it. It is perhaps symptomatic that Evans did not attempt to deal with the group in his masterly revisions of the Puerto Rican Lejeuneaceae! Equally symptomatic is the fact that the North American species, which are much better understood than the tropical ones, are still so poorly known that the material used to validate reports of species of this genus from Florida, in a recent extensive published list, are more than fifty per cent misdetermined, in many cases to the wrong genus! On a world-wide scale, it is prob-

able that the number of valid species will fall below one-half the number currently listed when the genus is properly monographed.

Although the group is not large in number of species in the United States, the species are quite polymorphic. Therefore, it is usually pointless to attempt to determine fragmentary material, or sterile plants (even when abundant), except at the periphery of the range of the genus, where so few species occur that fertile material is not necessary for determination.

The inherent polymorphism manifests itself in several characters that are widely used taxonomically: (1) the form and size of the lobule; (2) the size of the perichaetial bracts and bracteole (and the consequent degree to which the perianth protrudes beyond them, i.e. the degree to which the perianth is "exserted"); (3) the degree to which the bracteole is bilobed, and the form of its lobes (whether rounded or acute), and the degree of fusion with the bracts; (4) the size of the underleaves, especially as related to the size of the lobules.

Any diagnoses derived from these characters must therefore be drawn rather broadly. For instance, a variation in length of a hundred per cent in the perichaetial bracts in mature plants from the same patch (hence probably genotypically identical) is quite common in some species. An added complicating feature appears to lie in the tremendous degree of variation in size of underleaf, associated with degree of robustness of the plant. Unfortunately, relatively impoverished plants often bear androecia and perianths abundantly, and therefore tend to be regarded as "typical," while they actually do not represent typical manifestations (i.e. well-developed and optimally formed types).

Of the taxonomic characters here stressed, several have not been used in keys before, largely because the characters have been observed in too few species. Among such are the oil-bodies. The following tabulation, and critique of usefulness, of taxonomically important features, may prove helpful:

I. Vegetative Characters

1. *Underleaf size.*—Within limits, the form of the underleaf is taxonomically significant (whether wider than long, as in *L. floridana*, or whether as long as or longer than wide, as in most of our other species). Furthermore, the degree to which the sinus descends is often significant. The size (as compared with area of the lobule) is important, if mature stems, with lobules developed to their maximum extent, are utilized; size is best expressed in width compared to width of stem. Finally, in the separation of some species (*L. patens* from *cavifolia*) the degree to which the marginal cells protrude is important, i.e., the degree to which the margins are "crenulate."

On the basis of the underleaves, four groups of species can be separated: (a) *L. flava*, with large, ovate, contiguous to imbricate underleaves somewhat rounded to cordate at base (Fig. XXVI: 4); (b) *L. cavifolia*, with rather large, rotundate, contiguous to imbricate underleaves, rounded at base (Fig. XXXIV: 3, 8); (c) *L. floridana*, with remote underleaves as in the next group, which are however much larger than in that group, with the lobes usually over 6–8 cells broad (Fig. XLIX: 2–3, 12); usually with a very distinct rhizoid-initial area;

(d) *L. glaucescens* and all our other species, characterized by remote and small underleaves, with lobes only 3–6 cells broad (Fig. XXX: 4; XXXV: 11–12; XLV: 2, 8; XLVIII: 8, 13). *L. longifissa* is an extreme derived type of this group—(Fig. XLII: 4, 6).

2. *Oil-body form and number.*—Two basically different types of oil-bodies occur in the subgenus *Lejeunea*, the *cavifolia*-type and the *flava*-type. The former is represented, among our species, by only *L. cavifolia* and *L. minutiloba*; in it the oil-bodies are numerous, minute and homogeneous (Fig. XXXIV: 4; XLV: 1). All other species in our area have oil-bodies of the *flava*-type (Fig. XXVI: 1–2; XXX: 3), i.e., larger, distinctly papillose-segmented oil-bodies that occur only 3–8, occasionally 10–15 per cell.[8] Ocelli never occur in true species of the subgenus *Lejeunea*, although they frequently are found at the bases of the lobes and lobules in the subgenus *Microlejeunea*.

The oil-body differences are of major systematic importance. They allow us to separate, for example, the otherwise distressingly similar *L. minutiloba* and *L. cladogyna*.

3. *Lobule size and form.*—The subgenus *Lejeunea* is notoriously variable in this respect. In some species (*L. flava*, *L. "patens,"* *L. cavifolia*) the lobules are normally saclike and inflated, on both fertile and sterile shoots (Fig. XXV: 4, 7; XXX: 6; XXXIV: 1). In our other species, there is a great deal of diversity in this respect, and in each of the remaining species variation occurs from "lobulate" leaves (i.e., leaves with well-developed and inflated lobules) to "elobulate" leaves (i.e., leaves with the lobules reduced to a minute basal fold, with a 1–2-, rarely 2–4-celled apical tooth near whose summit is borne the hyaline papilla.

In *L. minutiloba* inflated lobules are produced only rarely (var. *heterogyna*); this is true also of *L. cladogyna* (Fig. XLVII: 6–7; XLVIII: 10). In both of these species there is often a sharp dimorphism in lobule size, with most or nearly all leaves quite "elobulate", the lobule being a mere few-celled basal fold or ridge, while a few are large and inflated. In such cases no lobules of an intermediate type are found. In *L. glaucescens*, on the other hand, most gatherings show a considerable range (sometimes even on a single plant) from small, broadly triangular inflated lobules, to vestigial lobules, with all intermediate types present (Fig. XXXV: 1, 8–10).

There is a well-marked correlation between extremes of habitat and "suppression" of lobulate leaves. In *L. floridana*, plants from wet rocks, subject to inundation, are uniformly "elobulate." Plants gathered within three to four feet higher on a bank, under drier conditions, have a high incidence of lobulate leaves. In *L. longifissa*, normal forms show frequent lobulate leaves. However, narrow-leaved, extreme shade forms may have uniformly elobulate leaves. Such elobu-

[8] The figures and descriptions of the oil-bodies of *L. cladogyna* and *L. glaucescens* in Schuster and Hattori (1954) were taken from mixed collections. The *L. cladogyna* figure was based on a mixture of that species and *Rectolejeunea brittoniae*; the plant from which the cytological data and figures were derived belonged to the latter! Similarly, the material of *L. glaucescens* used for the descriptions and figures showed admixture between *L. minutiloba* and *L. glaucescens*; the descriptions and figures pertain to *L. minutiloba*.

late phases have also been seen in *L. glaucescens*. In contrast, on dry rock walls one may find *L. minutiloba* with uniformly elobulate leaves, even though plants from moister habitats, on bark, may show occasional inflated lobules.[9] In such species as *L. flava*, where truly elobulate leaves are never produced, the forms of humid, shaded sites show small, if more or less inflated lobules (length often only 0.15–0.2 times length of lobe), while forms from dry, partly insolated bark may have them large and 0.25–0.35 times the lobe in length. It is thus readily evident that little systematic use can be made of the form of the lobules of some members of this group.

An additional and, from the point of view of the systematist, unfortunate complication is introduced by the fact that several species appear to be polymorphous with respect to the lobule from one geographical region to the next. For example, in western Europe *L. lamacerina* exists in two marked phases, a typical form with uniformly lobulate leaves, and var. *azorica* in which the lobules are quite polymorphic, with many highly reduced (Greig-Smith, 1954). These extraterritorial forms of *L. lamacerina* all appear to agree in the blunt and straight, relatively short apical tooth of the lobule, which distinguishes them from *L. "patens"* with a longer, curved, apical lobular tooth (Buch, 1934; Greig-Smith, 1954). The North American plants which I would refer to *L. lamacerina* as a discrete geographical race have, however, essentially uniformly inflated lobules, as in typical *L. lamacerina*. They show in lobule form, and in particular the form of the lobular apex and apical tooth, all types of gradation between the "normal" *lamacerina* type and the "normal" *patens* type of lobule! The implications of this type of geographical polymorphism, for some future monographer, are distressing.

It should also be pointed out that in many species the primary or secondary axes, from which sexual branches arise, show a greater or lesser reduction of lobule development. The lobules should, in general, be studied on robust sterile axes.

4. *Leaf and stem cells.*—The size of the leaf cells, and degree to which trigones are developed, are characters of some significance. Unfortunately there is sufficient variation in both features, *within the species*, to restrict the usefulness of these features as systematic characters.

In two species, *L. minutiloba* and *L. cladogyna*, the leaf cells are unusually small, the marginal averaging only 13–17μ, locally up to 18μ, in tangential width. In all our other species the marginal cells are larger, averaging 18–23 (–25)μ or occasionally (*L. floridana*) 21–23 (26)μ. These differences are statistically wholly valid, *if* we keep in mind that comparable shoots must be studied. Exceedingly reduced, tertiary axes of all of the species may show leaves with deviant cell sizes. Therefore the cell measurements must be based on mature leaves, and on

[9] Collections have been made of *L. glaucescens*, *L. minutiloba*, *L. longifissa* and *L. floridana* with uniformly "elobulate" leaves. Such plants would all key out, except for *L. longifissa*, to *L. minutiloba* in the key of Frye and Clark (*l.c.*, p. 793). Inversely, *L. minutiloba* var. *heterogyna* has some large, inflated lobules; it would key out most nearly to *L. glaucescens*, or *L. cladogyna* in their key.

the basis of the averages of a number of measurements of series of cells. Dependent on robustness of the material, therefore, a variety of measurements can be obtained, most of which can be misleading.

The development of trigones is so bound up with environmental conditions that it is difficult to make statements which have much validity. However, some species (*L. minutiloba*) may occur under very dry conditions on coral rock walls, yet be perfectly leptodermous and devoid of distinct trigones: inversely, such species as *L. flava*, *L. longifissa* and *L. cavifolia* may occur under relatively sheltered and humid conditions, yet show very distinct trigones and intermediate thickenings! Variation with extreme environmental conditions is so great in this respect that it appears unsafe to rely on these features to any extent.

The cortical cells of the stem are very variable in size, dependent on the robustness of the shoot. In almost all of our species the two rows of ventral cortical cells, which are easily measured, average 23–32μ in width per cell, with extremes of 16μ and 36μ. The isolated species, *L. floridana*, is at once distinct in that the ventral cortical cells are much more prominent, averaging 38–56μ in width.

5. *Texture.*—Several of our species (*L. minutiloba*, *L. cladogyna*) are strongly shiny when dry. Others (*L. glaucescens*, *L. floridana*) are quite dull when dry. To a limited extent, the texture of the leaves is a valid and useful specific character. Unfortunately, some species (*L. flava*) vary to a slight extent in this respect.

II. Reproductive Characters

1. *Position of the gynoecia.*—In *L. cladogyna* and *L. glaucescens* the perianths are considered to be invariably "cladogynous," i.e., restricted to abbreviated lateral branches (Fig. XXXV: 1; XLVIII: 10); in our other species they often occur on elongated leafy branches ("acrogynous"), but may occur in part on abbreviated lateral branches (Fig. XXV: 3–4; XLII: 7–8; XLVI: 4). Evans (1918) indeed relied on this restriction in position of the gynoecia as one of the major characters of *L. cladogyna*, as is reflected in the species name, and had emphasized the similar restriction of gynoecia in *L. glaucescens*. Unfortunately, prolonged study of large masses of material demonstrates conclusively that even these two species show occasional acrogynous inflorescences! It is true that only one or two such gynoecia have been found in *L. cladogyna*, but they are not at all rare in the varieties *acrogyna* and *obsoleta* of *L. glaucescens*, and indeed occur sporadically even in more or less typical *L. glaucescens*.

As a consequence, the utilization of the position of the gynoecia as a species character loses much of its imputed value. This, as well as almost all other characters that have been studied, "fail" with the prolonged examination of material.

2. *Gynoecial innovations.*—In the genus *Lejeunea* there is supposedly only a single subfloral innovation, whether the gynoecium is terminal on an elongate leafy shoot, or on an abbreviated lateral branch (Fig. XXV: 3–4; XLII: 7–8). Indeed, this is one of the features supposedly separating *Lejeunea* from *Hygrole-*

jeunea. Furthermore, when the gynoecia are cladogynous the single innovations, although often again fertile (not so usually in *L. cladogyna*, where they are almost always short!), rarely are repeatedly fertile. In the latter case, a rather distinctly cymose orientation results, characteristic of *Taxilejeunea*. Eifrig (1937), in his treatment of *Taxilejeunea* has, however, pointed out that *L. flava* may have such a cymose orientation of gynoecia, and indeed questions whether *L. flava* might not better be placed in *Taxilejeunea*.

A *Taxilejeunea*-like inflorescence pattern is also characteristic, to some extent, of several of the other species in the genus: i.e., the primary gynoecia are cladogynous, and bear innovations that are again almost immediately, and often repeatedly, fertile. This is the case in *L. glaucescens* (Fig. XXXV: 1) and in British "*L. patens*" (*L. serpyllifolia*), and Dr. E. W. Jones assures me that British plants of *L. lamacerina* "often have a *Taxilejeunea*-like inflorescence, the perianth on a short side branch with a weak innovation on the outer side."

From the preceding, then, one would gather that solitary innovations are the rule in *Lejeunea*, and this is the case until one deals with the *L. lamacerina* complex! In the European *L. lamacerina*, paired innovations, which I prefer to refer to as gemminate innovations, are "never seen in British material" (*teste* Greig-Smith, *in litt.*) or occur rarely, "but this appears to be exceptional" (E. W. Jones, *in litt.*). Yet in the Appalachian material of this complex such gemminate innovations are very regularly produced, e.g. in *Schuster 38087*, *36621*, etc.!

The situation in the Appalachian plants is rather interesting: the leading shoots, or at any rate leading, leafy branches, each end in a gynoecium, which often (sometimes almost invariably) bears gemminate innovations. Each of these innovations is sooner or later fertile again, but the secondary inflorescences usually or invariably bear solitary innovations. In addition, the long, leading primary branches that end in gynoecia may also bear short lateral fertile branches, i.e. cladogynous inflorescences!

From this it is clear that *within Lejeunea* variability in position of the gynoecia is so great that the value of this character as a criterion for separating *Taxilejeunea* and *Hygrolejeunea* becomes very questionable. The variation *within the species* in *Lejeunea* is also so considerable that the position of the gynoecia, and the number of innovations developed, can hardly be regarded as a primary species criterion!

3. *Perianth form.*—Variation in perianth form is limited in *Lejeunea*. Although traditionally the species of "*Eulejeunea*" possess pentagonal perianths that are not or hardly dorsiventrally compressed, *L. longifissa* differs in the distinctly compressed perianth (Fig. XLII: 2–3).

The fundamental shape is obovoid. In some species the perianth, *sans* carinae, is widest in the middle (*L. cavifolia*), in others it is widest clearly beyond the middle (*L. flava*, *L. "patens"*, *L. lamacerina*). These differences are relatively slight, and hardly of other than secondary significance.

Perhaps more valid as a differential feature is the degree to which the perianth-keels are elaborated. In most of our species the carinae are smooth or merely crenulate with rounded, tumid marginal cells. In European *L. "patens"*

the carinae may be quite distinctly crenulate-denticulate with strongly produced cells, thus approaching *Crossotolejeunea* in this respect. This is rather exceptional within *Lejeunea*. In *L. floridana* (Fig. XLIX: 4) the carinae are somewhat dilated above, often to the point where the beak appears distinctly recessed, rather than being clearly terminal; to a much slighter degree this may also be the case in *L. longifissa*. In our other species, the carinae are not elaborated above, and the perianth is never obcordate, the beak being strictly terminal (Fig. XXX: 6).

The degree to which the carinae are produced is of some, if minor, significance. In typical, western European *L. lamacerina*, for example, the carinae are normally quite well-developed, with "long, strongly winged keels" (Jones, *in litt.*), while in Appalachian plants (e.g. in *Schuster 36621*, *36608*, *38087*; i.e., the plants with gemminate gynoecial innovations) the perianths are "very inflated and almost keelless" (Greig-Smith, *in litt.*) and "stouter and very weakly winged, whereas the British plants have rather slender a perianth and long, strongly winged keels" (Jones, *in litt.*). Are these differences of species significance? Greig-Smith "would regard . . . the material . . . as *lamacerina*" while Jones states his "immediate reaction would be to doubt whether it was really the same as . . . *lamacerina*." This quoted matter shows how distressingly complex the variability in this, and other features, may be in the species of *Lejeunea*!

4. *Perichaetial bracts.*—In one species (*L. cladogyna*) the bracts are fused for up to one-third of the length of the bracteole to the latter (Fig. XLVIII: 1–3, 10–12); in our other species they are fused for a much shorter distance to the bracteole, or are nearly free. In two species (*L. cladogyna*, *L. floridana*) the bracteole is only slightly bilobed or emarginate, with blunt or frequently rounded lobes (Fig. XLIX: 5–11); in our others, divided 1/4–3/5, with acute to subacute lobes. The bracts have nearly obsolete lobules in *L. floridana* (Fig. XLIX: 8–9, 11), less vestigial lobules in *L. glaucescens* and *L. minutiloba* with the length of the lobule usually less than half that of the lobe (Fig. XLV: 4–7); in *L. cladogyna*, *longifissa*, "*patens*," *cavifolia*, *flava*, and *lamacerina* the lobule is well-developed, usually considerably more than half the length of the dorsal lobe, and constitutes more than a slight fold (Fig. XXV: 1–2; XXX: 8, 10; XLII: 11–13).

Varying with the size of the bracts, the perianth is more or less exserted beyond them. *L. glaucescens* and *cladogyna* have the smallest bracts (and a perianth normally exserted for three-fifths or more of its length); in our other species, the bracts are usually longer, and the perianth is at most exserted for a third to a half of its length. In the first two species the bracts are distinctly shorter than mature leaves (and much smaller in area); in the other species, the bracts may be subequal in length to the leaves, or even longer and larger. There is an excessive degree of variation in this character, however, and it must be utilized with caution, after study of a series of inflorescences (and derivation of an average size, with elimination of the extremes).

A greatly complicating factor in the evaluation of the size of the bracts, and correlated extent to which the perianth is extruded, is the position of the gynoecium. Indeed, the *size* of the bracts, and degree to which the perianth is extruded,

are largely functions of the gynoecial position. It will be recalled that *L. glaucescens* and *L. cladogyna*, which have the smallest bracts, and most nearly exserted perianth, have supposedly wholly cladogynous inflorescences. In the other species, with in part acrogynous gynoecia, the bracts of acrogynous gynoecia are much larger, and the perianth is more immersed between them. However, in the species with gynoecia variable in position, the acrogynous inflorescences always bear larger bracts and more immersed perianths, the cladogynous inflorescences are short-bracted and bear longly emergent perianths! The occasional acrogynous gynoecia of the usually cladogynous *L. cladogyna* and *L. glaucescens* are also provided with relatively large bracts and much less emergent perianths! Therefore, bract size (and form), and degree of extrusion or immersion of the perianth should be discussed on the basis of position of the gynoecia! When Frye & Clark (*l.c.*; see key to species and diagnoses) draw minute distinctions between such species as *L. cladogyna* and *L. glaucescens*, and their neighbors, on the basis of bract size and extrusion of perianth, they are assigning an erroneously narrow range in variation to these taxa. Their key, for understandable reasons, fails to separate these species.

5. *Androecial size.*—In some species (*L. longifissa*, *floridana*, *flava*) the androecia may consist of over four pairs of bracts, and therefore acquire a spicate form (Fig. XLII: 8): they may terminate main shoots (Fig. XXV: 4) or long branches (*L. flava*), which may grow again vegetatively after their production, or occur on short lateral branches (*L. floridana*). In other species (*L. cladogyna*, *minutiloba*) the male bracts are in few, usually 2–4 pairs, form a very short, circular or button-shaped androecium (Fig. XLVIII: 10) which normally occurs on a short lateral branch which ceases growth with the production of male bracts; such branches usually have only 1–2 pairs of more or less reduced leaves below them. In *L. floridana* an intermediate condition occurs: the male branch is very short, usually with no normal vegetative leaves below it, but consists of up to 5–10 pairs of small bracts, and thus is spicate in form (Fig. XLIX: 4). As with the position of the perianths, the position of the androecia (whether on a very short lateral, or on a main shoot or long lateral branch) appears susceptible to variation, even on the same plant. For example, in *L. glaucescens* the bracts are often in 8–12 pairs, forming a slender lateral spike, although androecia with only 3–6 pairs of bracts are common. In either case, the androecia are on short lateral branches. Yet, in *L. glaucescens* var. *acrogyna*, androecia terminal on leafy shoots occur!

In the *L. lamacerina* complex we again find a distressing range in variation. As E. W. Jones has noted (*in litt.*) the male inflorescence of the Appalachian members of the complex "are far larger and more conspicuous" than in the British plants! The significance of this must be interpreted in the light of the other discrepancies that characterize these geographic races.

6. *Sexuality.*—All our species are bisexual (autoecious).

It is evident from the above outline that the species of the genus show exceptional variability. The student should, therefore, not expect to be able to deter-

mine all of his material, even when well-developed. The inference by Frye and Clark (1947, pp. 792–793) that some of the species are mere modifications or ecological phases may possibly be true in one or two cases; however, with intensive study, the abundance of genotypically discrete forms, especially in tropical and subtropical Florida, becomes quite clear. It seems probable that the number of species locally will be increased, rather than decreased, on careful study.

Although the species of the subgenus *Lejeunea* show such a high level of variability that their determination is often virtually impossible, the reality of these entities as species is impressed on the student after several months of intensive study, particularly when supplemented with field work. It is only after weeks of continual attention to the group that any "feeling" for species in the group develops. Until the species impress on the investigator their distinctive facies, and individual peculiarities, *Lejeunea* will remain a frustrating and challenging group. Intermittent and sporadic mechanical "keying" of material is almost impossible in this genus. To gain any definite concepts of the species, it is almost necessary to prepare sketches of the oil-bodies (or carefully to note their size, form and number), and then let the material accumulate until several scores of specimens are available for study. It is only with comparative study of series of specimens, and with knowledge of the cytological features of the material, that positive determinations become possible. The accurate work of A. W. Evans on the regional members of the group, in a variety of papers, is all the more amazing when one considers that Evans worked with dead material, and consequently did not have the added data derived from the cytological features. The writer knows of no instance where a higher level of scientific intuitiveness was exhibited.

CLASSIFICATION.—No adequate attempt has ever been made to arrange the species of *Lejeunea* in sections. This, indeed, is the primary task which will confront any monographer of this exceptionally difficult and technical genus. As an initial effort in this process, the following is offered. Our species fall into seven sections, which are believed to be natural taxa. The position of the gynoecia has not been extensively used in this synopsis, since it is believed to be much too variable to afford a natural basis for the classification of the species. Future study will surely augment the number of sections recognized, when the exotic species are considered.

SYNOPSIS OF SECTIONS REGIONALLY REPRESENTED

1. Ventral cortical cells (16) 23–32 (36)μ broad; rhizoids sparing, never forming a distinct disk at underleaf-bases; perianths with keels not subauriculate distally; underleaves as long as or longer than broad (exc. *L. calcicola*); female bracts with lobules distinct, at least their apices free; bracteoles obviously bilobed, with acute to blunt lobes..... 2.
2. Leaves with lobules uniformly well-developed, never dimorphic, never vestigial; their length usually (0.2) 0.25–0.6× that of lobe; lobes ovate-oblong to oblong to ovate-falcate, always considerably longer than broad; underleaves divided to within (3) 4–6 cells of the rhizoid-initial area; gynoecia occurring both on short lateral and long leafy shoots..... 3.

3. Cells with homogeneous, minute, numerous (30–60 per cell) oil-bodies.
Sectio Cavifoliae (*L. cavifolia*)
3. Cells with segmented, larger, few (3–8, rarely to 15) oil-bodies..... 4.
4. Underleaves subcontiguous to imbricate, 2.5–4 times as wide as stem, at least (3) 4–5× the area of the small lobules.....Sectio Flavae (*L. flava*)
4. Underleaves remote, up to 2.5 times as wide as stem, subequal in area to twice the area of the large lobules.
Sectio Lamacerinae (*L. lamacerina, L. serpyllifolia*)
2. Leaves with lobules reduced in size or obsolete, or dimorphic, at least some of them vestigial: the length of the larger no more than 0.25–0.3× the lobe length; underleaves divided to within (1) 2–3 cells of the rhizoid-initial area..... 5.
5. Leaves with lobules variable in size, but not sharply dimorphic; lobes ovate to dimidiate-ovate, widest near base, dilated rather strongly just above the antical base, clearly longer than broad; cells relatively large: 18–23 (25)μ on margins, with segmented oil-bodies; plants dull or nearly so.
Sectio Glaucescentes (*L. glaucescens, L. calcicola, L. setiloba*)
5. Leaves with lobules sharply dimorphic; the majority (or sometimes all) vestigial, a few usually well-developed and inflated; lobes ovate-rotund to obovate-rotundate, broadly rounded at apex, widest near or slightly above middle, narrowed basally; cells small: 15–17 (18)μ on margins; plants strongly shiny, small..... 6.
6. Oil-bodies segmented, few per cell, rather large; perianth strongly plicate in distal two-thirds, slender, longly beaked.
Sectio Cladogynae (*L. cladogyna, L. longifissa?*)
6. Oil-bodies homogeneous, (8) 12–30 per cell, minute; perianth plicate only in distal third, broadly obovoid, shortly beaked.
Sectio Minutilobae (*L. minutiloba*)
1. Ventral cortical cells (36) 38–56μ wide; rhizoids numerous, from well-developed circular rhizoid-initial areas; perianth keels very short, but slightly dilated above, the beak recessed; underleaves broader than long; female bracts with lobules obsolete, without a free apex; bracteole emarginate, with rounded to blunt lobes; oil-bodies segmented, few per cell.....Sectio Floridanae (*L. floridana*)

KEYS TO SPECIES

Three separate keys to the species are given here because no one key can adequately separate all material at all times. Since, in general, no single characteristic is absolutely constant, the separation of the species involves the utilization of a constellation of characters; in general, however, the initial criteria cited in any couplet are more important than the last distinctions given. In cases of doubt, utilizing one key to check on another is indicated. Taxa not present within the area, but which have been reported from it in recent years, are included in the key for purposes of comparison; for that reason, also, *L. setiloba* is included.

KEY TO FERTILE PLANTS

1. Leaves polymorphous or with uniformly small lobules; isolated, many (or all) lobules reduced to vestigial basal folds of 18 or fewer cells; largest lobules only 0.2–0.25× length of lobe; underleaves divided to within (1) 2–3 cells of rhizoid-initials..... 2.
2. Mature stems with ventral cortical cells (16) 23–32 (36)μ wide; perianths with keels not produced into low shoulders or horns, evenly rounded, the beak not recessed or slightly so; underleaves averaging as long as or longer than wide (exc. *L. calcicola*); ♀ bracts with lobules large to small, but never obsolete (always present as a distinct

process extending beyond keel); ♀ bracteole distinctly bilobed, with obtuse to acute lobes ..... 3.

3. Reduced or vestigial lobules (sometimes rare or absent!) with apex formed by 1 (2) cells at whose summit is the hyaline papilla; underleaves not longer than broad, or scarcely so, divided for 0.4–0.65 of their length (exc. in *L. longifissa* which has cells with distinct trigones and intermediate thickenings) ..... 4.

4. Cells normally lacking obvious trigones and intermediate thickenings; underleaves bilobed for 0.4–0.65 of their length, their lobes usually terminating in single cells, their sinus acute to narrowly U-shaped, rarely broadly lunate, their lateral margins normally unarmed; ♀ bracts with lobes more or less entire, rounded or obtuse (rarely apiculate) at apex; bracteole bilobed for ¼–⅔ of its length, the lateral margins always entire; perianth not compressed or barely so, and with antical keel sharp and long (like lateral) ..... 5.

5. Mature leaves more or less broadly ovate-rotundate to obovate-rotundate, broadly rounded at apex, strongly narrowed above antical base, their marginal cells 13–17 (18)μ near leaf-tips; immature leaves strongly obovate; leaves sharply dimorphic, or lobules all, or largely, vestigial; underleaves 100–200μ wide, not distinctly broader than long; mature shoots only 600–960μ wide; lobes and lobules of ♀ bracts usually rounded or at least obtuse; plants strongly shiny.... 6.

6. Perianth sharply keeled for 0.5–0.65 of its length, rounded to subtruncate at apex, the beak elongated, terminating in slender, narrow cells; ♀ inflorescences normally all cladogynous; ♀ bracts with lobules at least 0.6–0.75× the length of lobes, more or less connate at base with bracteole; underleaves up to 155μ wide, their lobes usually 4 cells broad at base; some lobules always inflated (extreme environmentally-induced phases excepted); oil-bodies few, medium-sized, segmented ..... *L. cladogyna*

6. Perianth keeled only in distal 0.3–0.35, broadly truncate at apex, the short beak composed of slightly elongated cells; ♀ inflorescences in part on leading, leafy shoots; ♀ bracts with lobules very small usually, normally 0.35–0.5× the length of lobes, nearly free from bracteole; underleaves up to 200μ wide, their lobes often 5–6 cells broad; oil-bodies numerous (usually 10–20 or more) minute, homogeneous ..... 7.

7. Lobules uniformly reduced to minute basal vestiges; underleaves usually 175–200μ wide, their lobes usually 5–6 cells broad.. *L. minutiloba*, typical

7. Lobules in part inflated (at least on some of the subfloral, sterile, innovations); underleaves as in *L. cladogyna*.... *L. minutiloba* var. *heterogyna*

5. Mature leaves ovate to dimidiate-ovate, 1.1–1.35× as long as wide, narrowly rounded to obtuse to apiculate at apex, widest just above the dilated antical base, their marginal cells 18–23 (25)μ; immature leaves usually similar to mature ones (obovate in *L. calcicola* only); cells with oil-bodies moderate in size, few (usually 5–12) and segmented; lobules polymorphic, at least in part, inflated on mature sterile stems; mature underleaves of main stems (150) 180–225 (sometimes to 250)μ wide; mature shoots 1000–1450 (1600)μ wide; plants dull to weakly shining ..... 8.

8. Underleaves of main shoots averaging as long as to slightly longer than wide, narrowed to base; leaves rounded at apex; leaves of immature shoots more or less ovate like mature leaves, widest virtually at base, the leaf not strongly narrowed above base. (*L. glaucescens*) ..... 9.

9. ♀ Inflorescences uniformly (or almost so) on short, lateral, leafless shoots; one subfloral innovation; androecia also uniformly on short, lateral, almost or quite leafless shoots; mature perianths exserted for at least half their length beyond the very short bracts. *L. glaucescens* var. *glaucescens*

9. ♀ Inflorescences usually on leafy, elongate shoots, more rarely on short,

lateral shoots; 1–2 subfloral innovations; androecia indiscriminately on short, leafless or elongate, leafy shoots; mature perianth only slightly emergent beyond bracts.....*L. glaucescens* var. *acrogyna*

8. Underleaves averaging distinctly broader than long, rounded to subcordate at base; leaves often more or less obtuse to apiculate at apex; leaves of immature shoots characteristically obovate, broadly rounded at apex, strongly narrowed near base. (Lobules usually vestigial; androecia as in *L. glaucescens*; position of ♀ inflorescences very variable: from short lateral to long leading branches).....*L. calcicola*

4. Cells with obvious trigones and frequent intermediate thickenings; underleaves bilobed for 0.6–0.8 of their length, the narrow lanceolate lobes usually 3–4 cells broad, almost invariably ending in 2 superimposed cells, their lateral margins occasionally unidentate or angulate, the sinus broad to lunate; ♀ bracts very large (the perianth less than half exserted), with lobes sometimes pointed or repand-dentate to subdentate; lobules of bracts elongate, acuminate-lanceolate or lingulate-bidentate, free for over (0.3) 0.5 of their length; bracteole bilobed for (0.35) 0.5–0.75 of its length, the lobes sometimes 1–2-dentate; perianth more or less obcordate, distinctly compressed; ♀ inflorescences variable in position. *L. longifissa*

3. Lobules all (or many) reduced, the vestigial ones with an elongate apical tooth 2 (less frequently 1 or 3–4) cells long, terminated by a hyaline papilla; underleaves variable, but most of them longer than broad, divided for 0.6–0.7 of their length by a U-shaped or lunate sinus, the lobes narrow and acuminate, usually 4 cells broad at base; cells quite leptodermous, with segmented oil-bodies; leaves ovate, narrowly rounded distally; shoots 750–1250μ wide; female inflorescences occurring indiscriminately on short lateral, or long leafy branches.

[*L. setiloba*] and *L. glaucescens* var. *obsoleta*[10]

2. Ventral cortical cells of main stems 38–56μ wide; perianths with keels produced into coarsely crenulate, low shoulders or weak horns, the beak appearing recessed; underleaves 200–350μ wide, clearly broader than long, the lobes 5–8 cells broad; ♀ bracts as long as or longer than perianths, with lobules obsolete, the bracteole emarginate, with rounded lobes; cells large: 21–23 (26)μ on margins, 25–28 × 33μ or larger medially, with few, segmented oil-bodies.....*L. floridana*

1. Leaves rather uniform: all, or all but exceptional leaves of sterile stems, with discrete, inflated lobules 0.25–0.6× the length of lobes (rarely a few reduced on juvenile shoots, but well developed on fertile shoots); ♀ bracts large: the perianth less than half exserted beyond bracts; bracts with lobules large, 0.6–0.9× the length of lobes; ♀ inflorescences at least in large part on long branches (acrogynous); mature underleaves divided to within (3) 4–6 cells of the rhizoid-initial region..... 10.

10. Underleaves at least twice as large as lobules; posterior leaf-margin not or weakly incised at juncture of keel and lobe; underleaves nearly contiguous to slightly imbricate; leaf (and underleaf) margins not crenulate or only faintly so..... 11.

11. Cells with numerous (40–60) minute, droplet-like, homogeneous oil-bodies; underleaves usually less than 250 (280–300)μ long and wide, 2–4× the lobules in area.....*L. cavifolia*

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[10] *L. setiloba* is not known north of Cuba; it and *L. glaucescens* var. *obsoleta* key out at this point. The former has dimorphic lobules, with frequent large and inflated ones; the latter has the lobules uniformly obsolete. *L. setiloba* has the obsolete lobules with apical teeth 2–4 cells long; the var. *obsoleta* of *L. glaucescens* has them only 2 cells long. Some forms of *Rectolejeunea phyllobola* may have uniformly vestigial lobules, whose apices bear apical teeth 2–3, rarely even 4, cells long; all such forms of *R. phyllobola*, if inadvertently keyed out to this point can be safely separated from all of our species of *Lejeunea* subg. *Lejeunea* by the much smaller marginal leaf cells, averaging only 13–15μ.

11. Cells each with few (5–12–18) segmented, obvious and larger oil-bodies which disappear in drying; underleaves usually 250 × 300μ or larger, generally at least (3–) 4× the lobules in size..*L. flava*

10. Underleaves not or little larger than mature lobules; posterior leaf-margins normally more or less incised at junctures of keel and lobe; underleaves quite distant; oil-bodies as in *L. flava*..... 12.[11]

12. Gynoecia almost constantly with 1 innovation; perianth sharply 5-carinate in the distal ½–⅗, appearing winged; androecia usually very small and inconspicuous; flattened leaves always broadly rounded at the apex. (Confined to Atlantic Islands and W. Coast of Europe)..... 13.

13. Lobules of chief stems strongly inflated throughout, free margin involute including apical tooth, about half the length (and ⅕–⅓ of the area) of the lobe, keel strongly arched and at the apex at right angles to the posterior margin of free dorsal lobe (thus sharply notched); apex of lobule with a prominent, curved apical tooth; underleaves and leaves usually strongly crenulate on margins; underleaves 0.8–1.0× the area of lobules; ♀ bracteole with sinus acute to obtuse; marginal cells of distal one-half of lobe *ca.* 14–16μ.
[*L. serpyllifolia*]

13. Lobules of chief stems less strongly inflated, the free margin often nearly plane distally, *ca.* 0.35–0.4× the length (and 1/12–⅛, on branches ⅛–¼, of the area) of the lobes; keel moderately arched, at the apex at an obtuse angle with free dorsal lobe margin, thus not sharply incised; apex of lobule with a straight, blunt tooth that is rarely incurved; underleaves and usually leaves hardly crenulate on margins; underleaves averaging 1.0–1.5× the area of lobules; ♀ bracteole with sinus usually or frequently obtuse; marginal cells of distal one-half of lobe *ca.* 17–20μ.....[*L. lamacerina* subsp. *lamacerina*]

12. Gynoecia most often acrogynous, frequently with 2 innovations (but cladogynous gynoecia all with 1 innovation); perianth usually inflated and with carinae weak, distinct in only distal ¼–⅓; androecia often large and conspicuous; leaves usually weakly falcate, broadly ovate, with the apices usually rather narrowly rounded. (Lobule often large, with arched keel, but apical tooth usually blunt and not or little curved; cells of margins of lobe 18–22μ; Appalachian).
L. lamacerina subsp. *gemminata*

KEY TO STERILE PLANTS

1. Plants of the Appalachian Mountains and the northeastern states..... 2.

2. Leaves not notched at juncture of keel and dorsal lobe; underleaves clearly larger (usually at least twice as large) as lobules; leaf and underleaf margins not or faintly crenulate..... 3.

3. Underleaves small, distant; lobules small, often obsolete, less than one-fourth of the lobes in length; oil-bodies few per cell, segmented; normally cladogynous.
[*L. glaucescens*][12]

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[11] The three taxa in the *L. lamacerina-serpyllifolia* complex are very technical; the following two couplets will not, in the case of extreme specimens, always prove adequate. See Table I (p. 164) for a comparison of the major characters, and also compare with the keys immediately following.

[12] *L. glaucescens* is included at this point for several reasons; it occurs (var. *acrogyna*)

3. Underleaves large, more or less contiguous; lobules large, about ¼–⅓ of the length of the lobes; oil-bodies numerous, minute, homogeneous; largely acrogynous. (Widespread, s. to N. C. and Tenn. in the mountains).....*L. cavifolia*

2. Leaves more or less notched at juncture of keel and dorsal lobe; underleaves not or barely as large as the large lobules; Appalachian..... 4.

4. Lobule about half the length of lobe, *ca.* ⅕–⅓ of its area (on mature leaves of main shoots); lobule at apex with tooth incurved, elongated, the lobule opening by a circular aperture; underleaves strongly crenulate, the sinus rounded to acute, the area 0.8–1.0× that of lobules.....[*L. serpyllifolia*][13]

4. Lobule *ca.* 0.35–0.4× the length, and 1/12–⅙ of the area of lobe (on mature leaves of main shoots); lobule at apex with tooth short, blunt, not curved, usually not strongly incurved, the lobule not opening by a circular aperture; underleaves hardly crenulate, the sinus acute to narrowly U-shaped, the area 1.0–1.5× that of lobules.....*L. lamacerina*

1. Plants restricted to the Coastal Plain of the southeastern states[14]..... 5.

5. Lobules always well-developed (even on fertile stems); 0.25–0.4× length of lobes; underleaves large, contiguous to imbricate, 2.5–3.5 times as wide as stem; oil-bodies segmented, few; cells with distinct trigones. (Widespread, from Va. to Texas to Fla.).....*L. flava*

5. Lobules, at least in part, obsolete (at least on fertile stems), if inflated rarely over 140μ long (then less than ¼ of the length of lobe); underleaves distant (usually separated by a distance in excess of their length); cells with trigones absent or vestigial (exc. *L. longifissa*)..... 6.

6. Cells without large trigones and intermediate thickenings, more or less uniformly thin-walled; underleaves as long or nearly as long as broad, but never conspicuously longer than broad, their sinuses descending for 0.4–0.65 of their length normally; underleaf lobes normally ending in single cells..... 7.

7. Plants small: 600–960μ wide, very strongly glistening; leaves short, orbicular-ovate to orbicular-obovate, very broadly rounded at apex; marginal cells of leaves 13–17 (18)μ, the median 18–21 (23)μ wide; lobules strongly dimorphic, the inflated few (or absent)..... 8.

8. Oil-bodies segmented, few (4–8, rarely to 10 per cell), rather large; ♀ inflorescences (almost) uniformly on short lateral shoots; underleaves very small, up to 155μ wide, the lobes almost uniformly 4 cells broad. *L. cladogyna*

8. Oil-bodies homogeneous, 8–32 per cell, minute and glistening; ♀ inflorescences in large part on long, leafy shoots; underleaves usually larger, to 200μ wide, the lobes then 5–6 cells broad.....*L. minutiloba*

7. Plants larger: mature shoots 960–1500 (1600)μ wide, usually almost dull when dry; mature leaves distinctly ovate or dimidiate-ovate, widest just above base, narrowly rounded or obtuse to apiculate distally, considerably longer than wide; marginal cells of mature leaves averaging 18–23μ, the median 23–26μ wide or more; oil-bodies few and segmented, conspicuous..... 9.

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on the inner Coastal Plain of North Carolina, and may eventually be found inward to the Appalachian gorges; and it has been reported from Tennessee. As I discuss elsewhere, the latter report is incorrect and refers to a species of *Taxilejeunea*, which, *if it is inadvertently keyed to Lejeunea would key out at this point.*

[13] *L. serpyllifolia* (*L. patens*) is included in the key, within brackets, because of the numerous reports of the species from North America. As is subsequently discussed, all of these reports appear to pertain to *L. lamacerina*.

[14] *L. flava* has been found a single time at the juncture of Piedmont and the Applachian Escarpment, in South Carolina; it differs from all the other regional species in the rounded to subcordate underleaf bases, on mature plants.

9. ♀ Inflorescences (usually) uniformly on short lateral shoots; sterile plants usually with largely inflated (though small and very broadly attached) lobules, only rarely with any reduced to minute basal folds of a few cells; perianths long-exserted, the bracts very short and small. *L. glaucescens*, typical

9. ♀ Inflorescences variable in position: some or many on elongate, leafy shoots; sterile plants (in part at least) with lobules reduced to minute, vestigial basal folds ..... 10.

10. Vestigial lobules (sometimes rare or lacking!) with apex marked by a solitary cell (tipped by the hyaline papilla); plants when mature usually 1100–1400μ wide; ♀ bracts large, the perianth less than half exserted ..... 11.

11. Cortical cells of mature stems (16) 23–35μ wide; underleaves up to 220 (250)μ wide; ♀ bracts provided with distinct lobules, free for some distance beyond the keel ..... 12.

12. Underleaves as long as or longer than broad; ♂ inflorescences on short lateral or elongate, leafy shoots; mature leaves ovate, with narrowly rounded apices. *L. glaucescens* var. *acrogyna*

12. Underleaves averaging clearly broader than long; ♂ inflorescences only on short lateral, leafless shoots; mature leaves, particularly below acrogynous ♀ inflorescences, dimidiate-ovate and pointed ..... *L. calcicola*

11. Cortical cells of mature stems 38–50μ wide or more; underleaves broader than long, on robust stems 250–350μ wide; ♀ bracts with lobules quite vestigial, reduced to a minute fold, not free beyond keel ..... *L. floridana*

10. Some or all lobules, when vestigial, with a conspicuous tooth formed of 2 (or sometimes 3–4) superimposed cells; plants smaller, to 960–1100μ wide; ♀ bracts very small: much smaller than leaves, the perianths long-exserted. *L. glaucescens* var. *obsoleta* (see also *L. setiloba*)

6. Cells with more or less distinct trigones and intermediate thickenings; underleaves conspicuously longer than broad usually, the lobes lanceolate, 3–4 cells wide at base usually, occasionally laterally armed, their lunate, broad sinuses descending for 0.6–0.8 of their length; underleaf lobes usually ending in 2 superimposed cells; perianths flattened, somewhat obcordate, with recessed beak; ♀ inflorescences variable in position, partially on elongate, leafy shoots ..... *L. longifissa*

KEY TO SPECIES (LIVING MATERIAL)

1. Oil-bodies minute (2–2.5 × 3–6–7μ or smaller), glistening, homogeneous, numerous (8–50 per cell) ..... 2.

2. Underleaves large, 2–3 times as wide as stem, approximate to imbricate; lobules large, uniformly inflated (even on fertile plants); female inflorescences often on long, leafy branches; oil-bodies less than 2 × 3μ, 40–60 per cell. Northern; in region of deciduous and coniferous forests ..... *L. cavifolia*

2. Underleaves small, 1.5–2 times as wide as stem, quite distant; lobules largely or entirely reduced to small basal folds; female inflorescences often on short, lateral branches; oil-bodies ranging up to 2–2.5 × 5–7 (9)μ, 8–32 per cell. Tropical and subtropical. *L. minutiloba*

1. Oil-bodies larger (the larger 3–5 × 6–10μ or even larger), formed of numerous discrete, more or less protuberant spherules, appearing papillose, or segmented, few (3–12) per cell ..... 3.

3. Leaves with lobules almost constantly well-developed, inflated (even on fertile plants); ♀ inflorescences frequently or usually on long leafy shoots, with the ♀

bracts longer than (or as long as) vegetative leaves; ♀ bracts with lobules well-developed, at least half the length of lobe ..... 4.

4. Leaves with posterior margin not, or hardly, notched at juncture of lobe and keel; lobule less than ⅓ of length of dorsal lobe; lobes and underleaves not or obsoletely crenulate; underleaves at least twice the size of the lobules, approximate to barely imbricate. Coastal Plain and tropical ..... 5.

5. Perianths rounded to apex, the beak not recessed; underleaves up to 350μ wide or more, 4–8× the lobules in size (or more); cells collenchymatous .... *L. flava*

5. Perianths with keels dilated above, the beak recessed; underleaves up to 220μ wide, 2–3× the lobules in size; cells more or less equally thick-walled.

See *Rectolejeunea*[15]

4. Leaves distinctly notched at juncture of keel and free dorsal lobe, the keel usually strongly arched; lobule ⅓–½ the length of dorsal lobe, large; underleaves 0.8–1.5 times as large as adjacent lobules, quite remote. Appalachian (above 2000 ft. southward) ..... 6.

6. Leaves with lobules of main stems small: their area 1/15–⅙ of that of lobes; lobes broadly ovate-triangular, hardly falcate, antical margin strongly dilated above the narrowed base; lobules with apical tooth usually short, blunt, straight or hardly curved; marginal cells of lobe averaging (16–17) 18–20 (22)μ; gynoecia in large part acrogynous, often almost exclusively so; posterior leaf-margin at juncture of keel and dorsal lobe slightly to moderately incised (angle: 160–90°); underleaves often with sinus U-shaped to broadly lunate .. 7.

7. Acrogynous gynoecia almost always with 1 innovation; cladogynous gynoecia predominant or frequent; androecia short, on short lateral branches; ♀ bracts with lobes partly broadly obovate, with lobules short (0.4–0.55 (0.6)× length of lobes); perianths deeply 5-carinate to below the middle. Leaves with lobules relatively small, with keel weakly arched usually, the free margin distally clearly evolute ..... *L. lamacerina* subsp. *lamacerina*

7. Acrogynous gynoecia frequently with 2 innovations; cladogynous gynoecia on short branches rare or absent; androecia occasionally longly spicate, on lateral or leading branches; ♀ bracts with lobes lingulate to oblong-obovate, with lobules elongate (0.55–0.75× length of lobes); perianths shallowly to sharply 5-carinate to the middle, but often hardly carinate and only near perianth apex. Leaves with lobules often larger, with keel strongly arched, free margin appearing largely involute.

L. lamacerina subsp. *gemminata*

6. Leaves with lobules of main stems large: their area 1/7–⅛ of that of lobes; lobes strongly falcate, falcately elliptical, the antical margin evenly arcuate from base to apex; lobules with margin strongly involute, including the long, curved apical tooth; marginal cells of lobe *ca.* 14–16μ; gynoecia largely on abbreviated lateral branches, never with 2 innovations; posterior leaf margin, at summit of the strongly arched keel, sharply incised (angle: 65–90°); underleaves with V- or narrowly U-shaped sinus; perianths deeply 5-carinate

L. serpyllifolia

3. Leaves with lobules, at least in part, reduced to small basal folds, at most up to 140–160μ long when inflated (in *L. glaucescens* sometimes largely with inflated, broad and short lobules), the length of the largest at most ¼ of the length of dorsal lobe; ♀ inflorescences commonly (or largely to entirely) on short lateral branches .... 8.

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[15] *Rectolejeunea phyllobola* and *R. brittoniae* are often confused with *Lejeunea;* the lobulate phases, if erroneously sought under *Lejeunea*, would key out to this point. Elobulate phases will hardly key out, but it should be recalled that all phases of the species of *Rectolejeunea* have very small marginal cells, usually only 12–15μ. Those of *Lejeunea* species are 15–19μ or even 18–24μ on the margins.

8. Perianths keeled only in distal 0.25–0.3, with keels produced distally into low angles or shoulders, the beak recessed; bracteole bilobed for ⅛–⅕, the lobes rounded; ventral cortical cells of stem large: on mature shoots 42μ wide or more; underleaves averaging wider than long; bracts barely to distinctly exceeding perianth, with obsolete lobules scarcely free at apex ..... *L. floridana*

8. Perianths with keels rounded into base of beak distally, not produced, the beak not or only partly recessed; bracteole bilobed for ⅕–⅖ with acute lobes; ventral cortical cells averaging 23–35μ wide on mature stems; ♀ bracts with distinct lobules, more or less free (at least at apex) .... 9.

9. Leaves of mature shoots more or less ovate, usually somewhat narrowed and narrowly rounded apically, broad basally, conspicuously longer than broad; marginal cells of mature leaves averaging (18) 20–23μ; female inflorescences often on elongate leafy shoots (exc. in typical *L. glaucescens*); plants medium-sized to robust, mature shoots 960–1400μ wide (exc. sometimes *L. longifissa*) ..... 10.

10. Obsolete lobules (if present) terminated by a 1 (–2)-celled apical tooth (whose apex may bear the hyaline papilla); underleaves little or no longer than broad, their lobes infrequently terminated by two superimposed cells (exc. *L. longifissa*) ..... 11.

11. Cells normally without trigones and intermediate thickenings; underleaves nearly as wide as long to broader than long, the lobes (4) 5–7 cells wide or more, terminated usually by solitary cells; sinus usually acute or nearly closed; perianth truncate at apex, but beak not recessed, not dorsiventrally compressed ..... 12.

12. Underleaves of main shoots averaging as long as or longer than broad (0.85–1.05 times as wide as long, by actual measurement), narrowed to base; leaves of slender sterile shoots not, or exceptionally, obovate, even the younger leaves normally strongly ovate, narrowed to apex ..... 13.

13. Perianths uniformly (or almost uniformly) cladogynous; androecia spicate, always on short lateral branches, often with 4–12 (15) pairs of bracts; ♀ bracts short, the perianth longly exserted ..... *L. glaucescens*

13. Perianths often on long, leafy shoots (and with 1 or 2 subfloral innovations); androecia on lateral or long leafy branches, only with 4–5 (6) pairs of bracts; ♀ bracts elongate, as long as leaves, the perianth shortly emergent beyond bracts. *L. glaucescens* var. *acrogyna*

12. Underleaves averaging broader than long (1.1–1.35 times as wide as long, by actual measurement), rounded or subcordate at base; occasional leaves apiculate or subacute; leaves of slender shoots normally more or less strongly obovate, with the basal 0.3–0.5 strongly narrowed, the apex broadly rounded; otherwise as in *L. glaucescens acrogyna* ..... *L. calcicola*

11. Cells normally with obvious trigones and intermediate thickenings (best developed in bracts and perianths); underleaves elongate, with lanceolate lobes 3–4 cells wide, frequently laterally angulate, usually terminated by 2 superimposed cells, the sinus more or less broadly lunate or U-shaped; perianth obcordate, the beak recessed, strongly dorsiventrally flattened ..... *L. longifissa*

10. Lobules all or mostly obsolete: the obsolete ones commonly terminated by an apical tooth formed of 2–3 superimposed cells (less commonly of 1 or 4) cells, at whose apex occurs the hyaline papilla;

underleaves often slightly to distinctly longer than wide, their lobes very narrow, almost uniformly 4 cells wide at base, occasionally laterally angulate, usually terminated by 2 superimposed cells; ♀ inflorescence on both short lateral and long leafy shoots.
L. glaucescens var. *obsoleta* (see also *L. setiloba*)

9. Leaves of mature shoots suborbicular-ovate to orbicular-obovate, very broadly rounded at apex; marginal cells averaging 13–17 (18)μ; ♀ bracts with lobules elongate, usually at least 0.6× length of lobes, united for most of their length with lobes; ♀ inflorescences uniformly cladogynous. Plants very small, strongly shiny, 600–960μ wide.
L. cladogyna

Lejeunea flava (Swartz) Nees

Jungermannia flava Swartz, Prodr. Fl. Ind. Occ. 144, 1788.
Lejeunea flava Nees, Naturg. Eur. Leberm. **3:** 277, 1838; Evans, Bull. Torrey Bot. Club **38:** 207, 1911; Schuster and Hattori, Jour. Hattori Bot. Lab. No. **11:** 47, pls. II: 22–23, X: 1–2, 1954.
Lejeunea Moorei Lindb., Acta Soc. Sci. Fenn. **10:** 487, 1875.
Jungermannia serpyllifolia Wilson and Hooker, *p.p.*; Drummond, Musc. Amer. St. Merid. 172, 1841 (not of Dickson).
Lejeunea serpyllifolia Sullivant, Musc. Alleg. No. 272, 1845 (not of Libert).
Lejeunea thymifolia Gottsche, Mex. Leverm. 314, 1867.
Lejeunea cavifolia Austin, Hep. Bor.-Amer. No. 97, 1873 (in part; not of Lindberg).
Lejeunea serpyllifolia var. *americana* Lindberg, Acta Soc. Sci. Fenn. **10:** 486, 1875 (in part).
Lejeunea americana Evans, Mem. Torrey Bot. Club **8:** 154, pl. 20, figs. 14–26, 1902; Buch, Rev. Bryol. (n.s.) **61:** 239, 1934.
Lejeunea (*Eu-Lejeunea*) *flava* subsp. *albida* Spruce, Hep. Amaz. et And. 269, 1885.
Eulejeunea flava Schiffner, *in* Engler-Prantl, Nat. Pfl.-Fam. **1**(3): 133, 1893; Schiffner, Conspect. Hep. Arch. Ind. 249, 1898.
Lejeunea (*Eu-Lejeunea*) *flava* Spruce, Hep. Amaz. et And. 268, 1885.
Lejeunea cavifolia Frye and Clark, Univ. Wash. Publ. Biol. **6**(5): 795, 1947 (in part; at least as regards citation of most specimens).

Plants in depressed, *pale or whitish yellow-green patches, more or less weakly shiny when dry*, closely appressed to substrate, but only loosely attached by rather sparse rhizoids; mature shoots mostly *900–1300 μ wide*, sparingly and irregularly pinnately branched. Stems 70–90μ in diam., 1–5 cm. long; cortical cells in 7 rows, 25–30 (35)μ wide × 36–45μ long, (12) 15–20μ thick radially, somewhat thick-walled (the radial walls, and walls between cortical and medullary cells rather strongly thick-walled; the outer, free walls less so); medulla of a peripheral row of 7–8 cell-rows, surrounding 3–4 interior cell-rows, the medullary cells *ca.* 12–15μ in diam., thin-walled or slightly thick-walled, especially at the angles. Leaves slightly to moderately imbricate, *nearly plane*, the *lobe relatively narrowly ovate to oblong-ovate* (from 420–460μ long × 310–320μ wide to 490–510μ long × 400μ wide, occasionally up to 600–625μ long × 450–475μ wide), *the length 1.24–1.38× the width*, widely spreading (usually 55–85°), rounded or broadly obtuse at apex, the margins entire or vaguely crenulate owing to barely projecting cells; antical margin arching across or barely beyond the stem, slightly rounded at base; postical margin somewhat less arched, forming a very obtuse angle with keel (the *posterior margin only shallowly and broadly notched at juncture of keel and free dorsal lobe*). Keel rather weakly arched, occasionally moderately convex, 100–125μ, rarely up to 155μ long. *Lobules uniformly inflated, small (area usually 0.1–0.4× that of underleaves)*, ovate or ovate-triangular, obliquely to widely spreading, 85–90, occasionally up to 150 (in xeromorphic extremes rarely up to 200)μ long × 80–100, rarely up to 140μ wide; free margin strongly involute, the obtuse apical cell only slightly discrete without flattening of lobule; sinus between apical tooth and keel shallow, usually strongly oblique. Cells of lobe only

slightly convex, thin-walled, in distal portion of leaf with usually minute or small trigones and only occasional intermediate thickenings, *in basal half of leaf usually with nodular intermediate thickenings and trigones*; marginal cells of leaf-apex mostly 16–20μ, median cells; 18–21 × 20–24 (29), rarely up to 22–25 × 24–30μ, basal collenchymatous cells 23 × 23–30μ; oil-bodies 3–15, but *usually 5–12 per cell*, varying from fusiform to elliptical and 2 × 3.5–7μ to 3 × 4μ, up to 4–5 × 5–10μ, in occasional cells largely spherical and 2.8–3.2μ, *distinctly but finely segmented* (spherules 0.5–0.8μ or less usually; exceptionally coarser and 1.2–1.5μ in xeromorphic extremes); chloroplasts *ca.* 3.2–3.5μ, rarely up to 3.5 × 5μ.[16] *Underleaves very large, usually contiguous to imbricate*, their area usually 3–6, occasionally 6–12× that of the adjacent lobules, usually 0.3–0.7× that of the underlying lobes, ovate-orbicular to orbicular, 225–255μ wide × 230μ long up to 265–280μ wide × 250–275μ long, occasionally up to 330–375μ wide × 345–375μ long, *rounded or subcordate at base*, divided to about half their length into erect, triangular lobes, acute or apiculate at apex, *usually 8–10 cells wide at bases of lobes*; sinus acute and narrow, or subacute with narrowly rounded or obtuse base; margins entire or slightly sinuate, not or indistinctly crenulate; underleaf cells *ca.* 17–23 × 19–27μ.

Autoecious, abundantly fertile. Androecia either on short lateral branches, or on leading, leafy branches (in the latter case often becoming intercalary); bracts in usually 3–6, occasionally up to 8 pairs, somewhat smaller than vegetative leaves, subequally bilobed, rather closely imbricate (the androecia, when elongate, distinctly spicate). ♀ inflorescence most frequently on leading leafy branches (becoming pseudolateral through the development of a strong innovation; more rarely with innovations on both sides), less frequently on short lateral branches (then with only 1 innovation); innovations often repeatedly floriferous. Bracts *large* (as long as or longer than vegetative leaves), somewhat complicate; lobe oblong to narrowly or broadly obovate, broadly rounded at apex, less frequently obtuse or subacute, up to 600μ long × 240–300μ wide; *lobule large, usually oblong to ovate-lanceolate, rounded at apex* (the rounded apex sometimes with a slight emargination in which is situated a hyaline papilla), 350–400μ long × 165–180μ wide; bracteole more or less free, ovate to oblong-ovate, 550–570μ long × 300–350μ wide, bilobed up to the middle, the lobes erect, acute to obtuse, the sinus narrow and sharp. Bracts and bracteole of cladogynous inflorescences often smaller; bracts with lobe only 460–470μ long × 255–305μ wide; lobule 320–340μ long × 150–160μ wide; bracteole 450μ long × 290μ wide. Perianth *obovoid, usually more or less dilated above the middle*, sharply 5-carinate in the upper 0.3–0.5, up to 350μ wide × 700μ long, the *keels dilated*, suddenly narrowed distally, the *apex thus broad and more or less truncate*, the short beak, however, not recessed; lateral keels usually sharper, frequently slightly winged, the keels smooth. Spores 14μ in shorter diameter.

TYPE: Jamaica (*Swartz*); at least part of the type is in the British Museum of Natural History (*fide* Evans).

DISTRIBUTION.—A very widely distributed, polymorphic, pantropical species. The type came from Jamaica, but the species appears to occur throughout the West Indies (Puerto Rico!, Jamaica, Virgin Isls., Guadaloupe, Cuba!, the Bahamas!, Trinidad), northward to Bermuda!, southward from Mexico to Guatemala, Honduras and Panama, into the northern half of South America (from which it was reported by Spruce). In our region occurring from Florida to Texas, northward to North Carolina, and extreme southeastern Virginia.

Apparently widespread in South Africa (Arnell, 1953), the Atlantic Islands (Canaries, Madeira, Azores), northward to the hyperoceanic portions of Europe (Ireland!). Also widespread in Asia, from Japan (*Hattori*!), to Java and Sumatra,

[16] The cytological data (cell size; oil-body size, number and shape) all derived from the populations of the southeastern United States.

and eastward to Australia, New Zealand and Samoa. Concurrent with the great dispersal of the species there is a high level of polymorphism, expressed in the size of the lobule (respective to the underleaf and lobe sizes), shape of the underleaf and perianth-keels, and also in the cell size (see Greig-Smith, 1948). These differences are to a large extent geographically correlated, with the consequence that racial segregation seems warranted. This segregation is attempted in the discussion of variation subjoined; the following local reports all belong to the typical race, or subsp. *flava*.

Florida: MARION CO. (Juniper Creek, Ocala Ntl. Forest, *RMS 33395h, 33396a*; Juniper Springs, Ocala Ntl. Forest, *RMS 22468, 22618a*; Oklawaha R., 4 mi. e. of Silver Springs, *RMS 22506*); LAKE CO. (Alexander Springs, Ocala Ntl. Forest, *RMS 33512, 3302a*); DADE CO. (Paradise Key, Everglades Ntl. Park, *RMS 20184a, 19930, 19931, 20153a, 19936, 22590b*; Costello Hammock, near Silver Palm, *RMS 22958, 22961*; hammock in Long Key Pineland, 3.5 mi. n.w. of Paradise Key, *RMS 36819d, 36835, 36801e, 36818a*; Timms Hammock on Bauer Drive, on leaves of *Tectaria heracleifolia, RMS 33701-h, p. p.*, with *Aphanolejeunea evansii, L. minutiloba, Rectolejeunea phyllobola, Cololejeunea minutissima myriocarpa, C. subcristata, Caudalejeunea;* hammock in Long Key Pineland, Sect. 24, Everglades Ntl. Park, *RMS 22145*; Mathesson Hammock, near Cutler, *Schuster*; Mahogany-Royal Palm Hammock, just s.w. of tip of Long Pine Key, Everglades Ntl. Park, *RMS 37355a, 37302, 37306 p.p.*); HIGHLANDS CO. (Highlands Hammock State Park, w. of Sebring, *RMS 19941a*); HILLSBOROUGH CO. (Hillsborough R. State Park, *RMS 22781a*); HERNANDO CO. (s.e. of Brooksville, *RMS 22735a, 22729a*); COLLIER CO. (Collier-Seminole State Park, *Schuster*; Naples, *Grout*); LEON CO. (Lena Stein Hammock, *Schornherst*); SEMINOLE CO. (Sanford, *Rapp!*); POLK CO. (Clark's Pool near Lakeland, on *Magnolia virginiana, Sharp, 1948*; Bay head on Crystal Lake Road, *Redfearn, Dec. 1948*; 5 collections studied, 4 of which determined and listed by Redfearn [1952] as "*Lejeunea cavifolia*"; on citrus, Winter Haven, *McFarlin 584!*; Lake Rosalie, *McFarlin 552!*; Kissinger Springs, *McFarlin 6*, a mod. *leptoderma* with unusually narrowly oblong lobes, small lobules less than 0.05 × the lobes in area, and rather elongate underleaves); HARDEE CO. (2 mi. e. of Wauchala, *Redfearn, July, 1949*; 2 collections studied, reported by Redfearn [1952] as "*Lejeunea cavifolia*"); ST. JOHNS CO. (St. Augustine, *Haynes 2166!*); also reported from CITRUS, LEE, MANATEE, PASCO, SEMINOLE and VOLUSIA COS. (*Redfearn, 1952*). **Georgia:** LIBERTY CO. (St. Catherine's I., *Morrison, 1939!*; Half Moon Landing, *Morrison 39–23!*; Midway, *Blomquist 11521!*); THOMAS CO. (*Brown!*); DOUGHERTY CO. (near Thomasville, *Anderson 5183!*); CHARLTON CO. (Okefenokee Swamp, *Blomquist 11503!*); BRYAN CO. (Ft. McAllister, *Morrison 39–13!*). **South Carolina:** Near Charleston (*Wagner!*); AIKEN CO. (Clearwater Swamp, near Augusta, *Blomquist 9068!*; near Aiken, *Batson!*). **North Carolina:** COLUMBUS CO. (e. of Whiteville, *RMS 30040, 29211a, 29241, 29481*); PENDER CO. (near Wilmington, *Patterson 1423!*); WASHINGTON CO. (near Roper, *RMS 28359, 28365*; e. of Plymouth, *Anderson 5975!*); DARE CO. (Collington, *RMS 28313*; 5–8 mi. s. of Manns Harbor, *RMS 28381*); BRUNSWICK CO. (Smith I., *Anderson 6820; Schuster and Blomquist*; Orton Plantation, *Blomquist 14863!*; near Holden Beach, *Blomquist 7358!*); DUPLIN CO. (w. of Wallace, *Anderson 3893*); ROBSON CO. (Red Spring, *Gray 7446!*); BLADEN CO. (swamp, w. Bladen Co., *Blomquist 7125!*); CARTERET CO. (Bogue Banks, s. of Atlantic Beach, *Jones 2616!*); BEAUFORT CO. (near Washington, *Blomquist 6003!*; Waccamaw R., near Old Dock, *Anderson and Evans 6184!*; w. of Lake Waccamaw, *Blomquist 7369!*). **Virginia:** NORFOLK CO. (n.e. corner of Lake Drummond, in Dismal Swamp, *Schuster and Patterson 34563 p.p., 31554, 34558*).

Alabama: MOBILE CO. (near Chunchulla, *Schuster*). **Mississippi:** WAYNE CO. (13 mi. w. of Waynesville, *Anderson 5381!*); HARRISON CO. (5–7 mi. s. of Ramsey Springs, *RMS 27771;* near Handsboro, w. of Biloxi, *RMS 20404, 20399a; Magnolia-Ilex-Quercus nigra* forest 7 mi. s. of Ramsey Springs, n.e. corner of county, on bark of *Ilex opaca*, with *Chiodecton sanguineum, Harpalejeunea ovata, Cheilolejeunea rigidula, RMS 27788*); GEORGE CO. (Wyatt Hills,

n.e. of Ramsey Springs, w. George Co., *RMS 27691f, 27694*); SIMPSON CO. (2 mi. e. of Rte. 49, near Saratoga, *RMS 19167c*); JACKSON CO. (2–3 mi. n. of Escatawpa, *RMS 19133;* Pascagoula R., 6–7 mi. n.e. of Van Cleave, *RMS 19220, 19229, 19238;* Black Creek, 7–8 mi. n. of Escatawpa, on base of *Nyssa sylvatica biflora*, *RMS 29235a;* a mod. *pachyderma* with nodular trigones and intermediate thickenings; same locality, on *Cyrilla racemiflora*, *RMS 29258*). **Louisiana:** Lake Charles (*Frye;* issued as *No. 9*, "Hepaticae, distr. by Clark and Frye," as *L. americana!*); St. Martin Parish (s.w. of Breaux Bridge, *Correll 9439!*); Avoca I.; Bateman's I.; Houma; Morgan City (*Svihla, 1926*, etc.); Cypress-tupelo gum swamp, New Orleans (*Pennebaker, Sept. 1939!*). **Texas:** ANGELINA CO. (Blue Hole, s.e. of Zavalla, *Whitehouse 22560!, p.p.*); HARRIS CO. (Houston, *Elihu Hall, March 30, 1878!*).

The above reports are all from the Coastal Plain. In addition to these stations, the species occurs as a rare and local relict in the "old tropical" gorges of the Southern Appalachian Escarpment, as follows:

SOUTH CAROLINA: PICKENS CO. (near mouth of ravine of Estatoe River, *RMS 37656, p.p.*).

The escarpment station is from a rich, mesic forest allied to the Mixed Mesophytic Forest, with *Rhododendron maximum*, *Leucothoë editorum*, etc.; associated on the dry boulders where the *Lejeunea* occurred were *Plagiochila undata*, *P. virginica*, *Leucolejeunea unciloba*, *Radula obconica*, *R. complanata*, etc.

ECOLOGY.—Occurring most frequently on bark, more rarely (in our area) over damp shaded rocks, or as an epiphyte on living leaves.

The exceptional regional occurrences on shaded damp rocks (as in Simpson Co., Miss.) are with the filmy fern, *Trichomanis petersii*, amongst and over which it grows, together with *L. minutiloba*, *Porella pinnata*, *Radula* sp., and *Plagiochila dubia*.

In the tropical hammocks of southern Florida rarely on fronds of *Tectaria heracleifolia*, with *Aphanolejeunea*, *Cololejeunea*, *L. minutiloba* etc.; also epiphyllous on fern stipes (of *Nephrolepis*); then usually associated with *Caudalejeunea lehmanniana*, as at Timms Hammock. Epiphyllous occurrences of the species are more frequent south of our area.

In our region the species is almost always corticolous. It has a wider tolerance than our other species of *Lejeunea*, occurring often under relatively xeric conditions (as for instance, on the bark of *Quercus virginiana* in the xerophytic, salt-spray Live Oak Climax behind sand dunes; then often with *Frullania kunzei*, *F. obcordata*, *Leptocolea cardiocarpa*, occasionally *Cololejeunea minutissima* and *Cheilolejeunea rigidula*). When on bark in more mesic forests it may occur over a wide variety of trees. For instance, in the tropical hammocks of southern Florida, on the twigs and branches of a variety of trees and shrubs, and on their trunks; among them, twigs of *Chrysobalanus interior*, associated with *Brachiolejeunea bahamensis*, *Caudalejeunea lehmanniana*, *Leptolejeunea elliptica*, *Diplasiolejeunea rudolphiana*, *Frullania riojaneirensis*, *Syrrhopodon parasiticus*, etc. Also on twigs of *Psychotria nervosa*, with the same associates. Also over the standing or fallen trunks of the palms *Sabal palmetto* and *Roystonea regia* (where the species is a pioneer, together with *Rectolejeunea brittoniae*, *R. berteroana*, *Leptolejeunea elliptica*, *Leptocolea cardiocarpa*, *Lejeunea bullata* and *laetevirens*, *Plagiochila hypnoides*, etc.); also on the trunks of *Elaphrium simaruba* (where the species

is a pioneer on rapidly exfoliating bark, together with *Aphanolejeunea evansii*, *Leptocolea cardiocarpa*, *Leptolejeunea elliptica*, *Caudalejeunea lehmanniana* and *Lejeunea laetevirens*, *L. bullata*, and other extreme pioneer species). Further northward equally ubiquitous, occurring over the bark of *Myrica cerifera*, *Persea borbonia*, *Quercus virginiana*, *phellos*, *laurifolia*, and *nigra*, *Magnolia grandiflora*, *Nyssa aquatica*, *Taxodium distichum*, *Fagus grandiflora*, *Cyrilla racemiflora*, *Ilex opaca*, *Nyssa sylvatica biflora*, and even on the bark of post-mature *Pinus taeda*!

On bark in relatively xeric forests the species occurs only near the base of the trees; in more mesic forests it often ascends into the main branches, particularly the widely spreading branches of Live Oak and Laurel Oak. It is frequently associated, under more xeric conditions, with *Frullania kunzei*, *obcordata*, and *squarrosa*, *Leucolejeunea clypeata*, *conchifolia* and *unciloba*, and with *Leptocolea cardiocarpa*, occasionally also with *Lejeunea bullata*, *Cheilolejeunea rigidula*, *C. polyantha* and *Ptychocoleus heterophyllus*. In more mesic forests, with *Ceratolejeunea laete-fusca*, *Radula obconica* and *caloosiensis*, *Mastigolejeunea auriculata*, and locally with *Neurolejeunea breutelii*, *Cololejeunea contractiloba* and *diaphana*, *Lejeunea laetevirens*, *Lopholejeunea muelleriana* and *subfusca*. However, *L. flava* is predominantly a species of more open and less mesophytic conditions than are characteristic of the latter series of species.

RELATIONSHIPS.—*L. flava* is one of the most isolated species of the genus *Lejeunea*. It exhibits, as Eifrig (1937) has pointed out, definite similarities to *Taxilejeunea*. I am not at all convinced that the species should not be assigned to this genus. Indeed, it can be stated with some certainty that the basis for distinguishing *Lejeunea* from *Taxilejeunea* is a largely artificial one without much merit. The complex formed by *Lejeunea* s. lat. (as used here), *Taxilejeunea*, *Potamolejeunea* and *Hygrolejeunea* is not divisible into definable, or even clearly natural units, using the position of gynoecia and number of innovations—the criteria now considered as of primary importance in the separation of these taxa.

Eifrig (*l.c.*, p. 87, fig. IV, 1a) illustrates a plant of *L. flava* to demonstrate the *Taxilejeunea*-like orientation of the gynoecia. However, it needs to be emphasized that this orientation can be nearly or quite matched in, for example, *Lejeunea serpyllifolia* or *L. lamacerina*. In essence we find that the leading stem may produce a terminal gynoecium, which innovates (usually once), the innovation becoming so dominant that it appears to form a continuation of the main stem. This innovation may be repeatedly fertile, leading to the production of a superficially very elongated leading stem of indeterminate length; actually it consists of a more or less elongate leading stem, together with the vigorous subfloral innovations. (In apparently all populations of *L. flava* we may find two subfloral innovations—this is also shown in Eifrig's figure of Javan material; in such cases one innovation is usually weaker, and forms a clearly lateral branch.) In addition to such "acrogynous" inflorescences, which are often considered "typical" of *Lejeunea*, there are numerous gynoecia, usually developed on short lateral branches, i.e., cladogynous gynoecia (Fig. XXV: 4). Eifrig's figure shows that these gynoecia at times occur also on elongate, leafy, lateral branches (in which

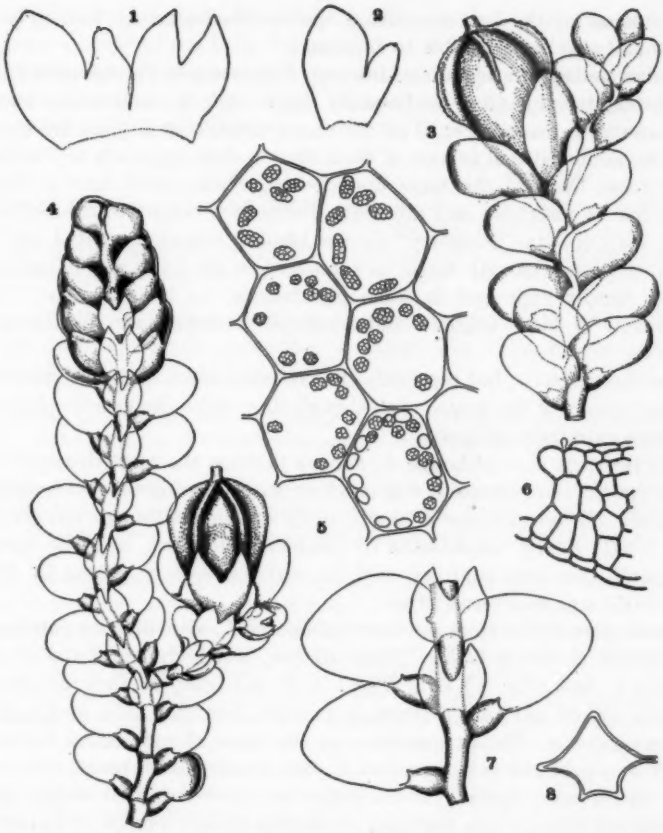

FIG. XXV. *Lejeuna flava* subsp. *flava* (Sw.) Nees. 1–2. Bracts and bracteole (×53); 3. Shoot with perianth and single innovation, dorsal view (×48); 4. Shoot with cladogynous perianth and terminal androecium (×31); 5. Median cells with oil-bodies, in lowermost cell also with chloroplasts drawn in (×735); 6. Apex of lobule (×185); 7. Postical aspect of robust shoot sector (×58); 8. Perianth cross-section, one third from apex (×31). (Figures all from *Schuster 19229*, Jackson Co., Miss.; all of the "*L. americana*" extreme.)

case they may bear fertile innovations), *but if they occur on short lateral branches the innovations are usually short and often remain sterile.* This latter condition I regard as the typical *Lejeunea* orientation of gynoecia: the cladogynous gynoecia, *which have been found in every species investigated* produce either short and sterile innovations, or at times innovations which are soon again fertile, *but without repeated fertility of these innovations.* (As is brought out in the introduction to this paper, these cladogynous inflorescences in *Lejeunea* usually innovate; if innovations are lacking, the plants should be relegated to the subgenus *Potamolejeunea*.) Using this criterion, *L. flava* can remain in *Lejeunea*, and, in point

of fact, many of the less specialized species illustrated as Taxilejeuneae by Eifrig would also be assignable to *Lejeunea*!

The above essay at a separation between *Lejeunea* and *Taxilejeunea* illustrates how thoroughly subjective—and equally vague—are the distinctions among the genera around *Lejeunea*. Yet, if all the characteristics of *L. flava* are evaluated, it must be admitted that certain of them show a close approach to *Taxilejeunea*. Among them are: (a) the large underleaves, whose bases have a somewhat arcuate line of insertion, and are quite distinctly rounded to subcordate (Fig. XXVI: 3–4); (b) the "tendency" for the lobules, although inflated and normal in form, to be exceedingly small, as compared to the lobes and underleaves—a tendency hardly expressed in some populations; (c) the "tendency "towards development of large trigones and numerous intermediate thickenings (Fig. XXVI: 7).

These three criteria, but especially the underleaf form, isolate *L. flava* from all our other species of the genus, even though they make the generic placement of the species extremely subjective.

DIFFERENTIATION.—Although *L. flava* is perhaps the most distinctive of the regional species of *Lejeunea*, it was much confused, during the last century, with *L. cavifolia* (*L. serpyllifolia* of many early authors, although incorrectly so). Evans (1902) clearly emphasized its distinctive features, and the species has consequently not been confused with *L. cavifolia* recently, except by Frye and Clark (1947) and Redfearn (1952).

Lejeunea flava differs from the totally allopatric *L. cavifolia* most fundamentally in the nature of the oil-bodies. These are few, relatively large, and clearly segmented in *L. flava* (Fig. XXV: 5; XXVI: 1–2); in *L. cavifolia* they are exceedingly numerous (30–60 per cell), extremely minute (less than 2.5μ long), glistening and homogeneous. The two species, on the basis of cytological features, can scarcely be considered as being allied. *L. flava* is also a paler plant, with a yellowish or whitish cast; typically, it has longer and narrower, more widely spreading and plane leaf-lobes; it has, normally, somewhat smaller lobules on mature leaves; and it possesses larger underleaves, whose bases are rounded or slightly cordate (Fig. XXVI: 3–4, 10–11). *L. flava* also has a more distinctly obpyriform-obconoidal perianth, with at least the lateral keels more strongly dilated and often narrowly winged (Fig. XXV: 3).

VARIATION.—Various authors have attempted to maintain two or more species in the *L. flava* complex. Evans (1902) considered the southeastern population to represent a separate species, *L. americana*, but later considered this to be a synonym of *L. flava*.[17] He states (1911, p. 207) that a portion of the type (from

[17] In spite of this, Frye and Clark (1947, p. 798) list *L. americana* Evs. as a synonym of *L. patens*! Furthermore, even though Evans (1902) clearly indicates that *L. flava* subsp. *albida* Spruce is a synonym of *L. americana* (and in 1911 again states that Spruce's *albida* agrees with both Floridean *L. flava* and the type material of *flava* from Jamaica), Frye and Clark state that Evans (1902) considered *L. flava* subsp. *albida* to be a synonym of *L. patens* Ldb. The synonymy they cite under *L. patens* is patently quite confused, and their concepts of the limits of *L. cavifolia*, *L. patens* and *L. flava*, as well as of *L. "americana,"* are totally unacceptable, judging from the material they cite under their "Examinations."

Jamaica) in the British Museum closely agrees with North American plants which had been considered to be *L. americana*.

Buch (1934) has again gone into the problem of the distinction between *L. americana* and *L. flava*, and considers them to be distinct. He would separate them by the following characters:

L. flava	*L. americana*
Lobules small, the lobe-area *ca.* 30× that of lobule.	Lobules large, the surface area of lobe *ca.* 5–12× that of lobule.
Underleaves 10–12× the lobule in area, *ca.* half the dorsal lobe in area.	Underleaves 4–6× the lobule in area.

However, study of numerous specimens has convinced the writer that any such distinction is virtually impossible to accept. The following specimens (and data derived from them) may be cited as evidence:

1. *J. A. Shafer 4483*, on wet rock, vicinity of Baracoa, Oriente, Cuba. Lobe-area 20–30× that of lobule; underleaves 8–12× the lobules in area; typical *L. flava*, shoots 900–1000μ wide.
2. Killarney, Ireland (*Schiffner*, Hep. Eur. Exsic. *1069*). Lobe-area 18–24, occasionally 24–30× that of lobule; underleaves 8–12× lobules in area. Typical *L. flava*, with narrow, widely spreading dorsal lobes and somewhat imbricate underleaves; plants up to 1250μ wide.
3. *Schuster 17859a*, Simpson Co., Miss. (Under very moist conditions, on damp rock, with *Trichomanis petersi*; the only specimen from eastern North America known from moist rock). Lobe-area 15–18× that of lobule; underleaves 6–9× lobules in size; plants up to 1200μ wide, with leaves spreading at angle of nearly 90° from stem. Nearly typical *L. flava*, but clearly intermediate to "*americana*" (Fig. XXVI: 2–3).
4. Timms Hammock, on Fern Stipe, Dade Co., Fla. (*A. J. Grout*). Lobe *ca.* 25–35× the almost vestigial lobules; underleaves 8–12, occasionally 16× the lobules in area. A "typical" *flava*, with unusually reduced lobules, from deep, moist floor of dense hammock forest (with *Caudalejeunea lehmanniana*); plants with lobes narrow, ovate-elliptical, spreading at right angles from stem; shoots up to 1100μ wide (Fig. XXVI: 10).
5. *Schuster 19229*, near Biloxi, Miss. (on relatively exposed bark at base of tree). Lobe-area varying from 8–12, rarely 16, × the area of the lobules; underleaf-area 3–4, rarely 5, × that of lobules; plants relatively small, with leaves spreading at an angle of only *ca.* 70°, with underleaves somewhat distant to approximated; shoots 670–760μ wide. (Plants clearly identical with *L. americana, sensu* Evans, 1902; closely matching Pl. 20, fig. 15 in Evans, 1902) (Fig. XXV).
6. *Blomquist 14863*, Orton Plantation, N. C., base of trees (in relatively xeric environment). Lobe-area 5–8, rarely 9–10, × that of the large, strongly inflated lobules (whose keels are quite arched); underleaves 2.5–4× the lobules in area. (Plant a clearly xeric form, shoots only 600–650μ wide; clearly identical with *L. americana* of Evans 1902, *but* with lobules somewhat larger and underleaves somewhat smaller).
7. Lake Charles, La. (on Oak Tree in woods; under evidently rather xeric conditions, since with *Polypodium polypodioides*), T. C. Frye. (Distributed as *Lejeunea americana*, in "Hepaticae; distributed by Clark and Frye, No. 9"; cited, as *Lejeunea cavifolia*, in Frye and Clark, 1947, p. 797).[18] Lobe 12–24× the lobules in size (the latter very variable in

[18] Frye and Clark (1947) cite five "Examinations" of *L. cavifolia*. Those from Lake Charles, La., and Timms Hammock, Fla., have been examined, and are reported on above; they represent good *L. flava*. The other two from the southeast (Pensacola, Fla.; Biloxi,

size); underleaves 6–10× the area of the lobules. A xeromorphic form, but moderately large in size (720–800μ wide), clearly a link between typical "*flava*" and typical "*americana*."

As is evident from a comparison of the above measurements, there is no clear break between "*flava*" and "*americana*" *sensu* Buch. For instance, of the above examinations, *Nos. 3* and *7* are clearly intermediate between *flava* and *americana*. When a long series of specimens is studied, it becomes evident that *L. flava sensu* Buch (i.e. the larger, more luxuriant plant) is restricted largely to mesic environments, often on moist rocks, or epiphytic on leaves, or on fern stipes in deep, moist tropical hammock forests. Both Swartz's type and the Grout specimen from Timm's Hammock, Fla., for instance, occurred on old leaves of ferns. On the other hand, "*L. americana*" is largely a species occurring on bark, often under relatively xeric conditions (as is typified by a collection made 6–9 feet above ground, on the horizontal branches of *Quercus virginiana*, on Smiths I., N. C., associated with the xerophytic fern, *Polypodium polypodioides*).

The writer is convinced that the mesic extreme of the species ("*flava*") is robust, up to 1.25 mm. wide or more, with large dorsal lobes and smaller lobules, widely spreading and relatively narrow leaves (Fig. XXVI: 3). With progressively more xeric conditions, a progressively more xeromorphic phase is produced, in which we find reduction in size (down to 600μ wide), with the dorsal lobes reduced in size, the lobules becoming larger and more strongly inflated, with a convex, arched keel, and with the reduced dorsal lobes more erect-spreading (Fig. XXV). This xeromorphic phase is considered to be *L. "americana."* The differences in facies the species undergoes in proportion with these changes are very considerable. For instance, in the "*flava*" extreme, the lobules are often only 0.2 of the length of the dorsal lobes. By contrast, in the smaller plants of the "*americana*" extreme, the lobules may be 0.3–0.35, rarely even 0.4 times the length of the dorsal lobes.[19]

Miss., both collected by Frye) are clearly *L. flava*. Only the specimen from New York represents *L. cavifolia*.

It should be kept in mind that these specimens of *L. flava* do not key to *flava*, but key to *L. cavifolia* in the key in Frye and Clark (p. 793), because of the unfortunate selection of key characters in that work. Only the mesic, lax, large-leaved extreme of *L. flava* will correctly key out in that work; since this plant occurs largely on wet shaded rocks, which are rare or lacking in the coastal plain of the Southeastern United States, it is further evident that most regional material of *L. flava* will key to *L. cavifolia* in Frye and Clark.

Although Frye and Clark cite *L. americana* as a synonym of *L. patens*, the material they distribute of *L. americana* is later cited as "*L. cavifolia*." This is one of a very few specimens of "*L. cavifolia*" Frye and Clark (*nec auct.*) which they examined, and upon which they base the contention that *L. planiuscula* (or *L. cavifolia* var. *planiuscula* as they have it) is invalid. They state: "From our examination of American material we were led to conclude that the variety *planiuscula* grades into the species (i.e., *cavifolia*) and should be dropped." Since their specimens are all but one *L. flava*, they obviously have no basis whatsoever for stating that *L. cavifolia* and *planiuscula* grade into each other. As will be discussed under *L. cavifolia*, *L. planiuscula* is related more closely to *L. serpyllifolia* than it is to *L. cavifolia*, and is indubitably a good species.

[19] The disjunct material from the Estatoe R., in the Blue Ridge Escarpment, is atypical

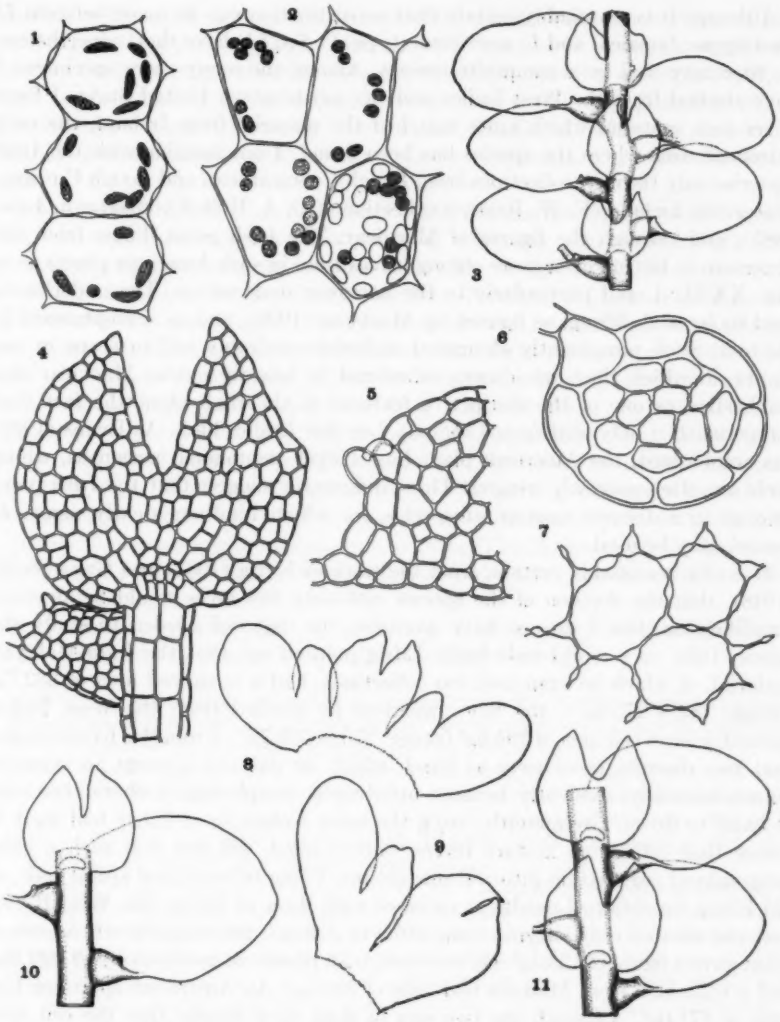

FIG. XXVI. *Lejeuna flava* subsp. *flava* (Sw.) Nees. 1–2. Median cells with oil-bodies, one cell also with chloroplasts (1, ×765; 2, ×670); 3. Postical aspect of robust shoot, of mesic phase of maximal size, epiphyllous form; lower left lobule with rotifer (×39); 4. Underleaf and lobule (×165); 5. Lobule apex (×265); 6. Stem cross-section (×395); 7. Basal cells (×540); 8. Bracts and bracteole from immature inflorescence (×42); 9. Mature bract and bracteole (×45); 10–11. Shoot-sectors, postical view (×61). (Fig. 1, 4, *Schuster 22145*, Florida; 2–3, Simpson Co., Miss., *Schuster 17859a*; 5–6, 7–9, 11, Paradise Key, Dade Co., Florida, *Schuster 19931*, *19936*; 10, Timms Hammock, Florida, *Grout*, on *Nephrolepis* stipe; figures all of the "flava" extreme.)

Although it is reasonably certain that no distinction can be made between *L. flava* (type: Jamaica) and *L. americana* (type: U. S.), I believe that, nevertheless, *L. flava* may well be a composite species. Among the many score specimens I have studied from the West Indies and the southeastern United States I have never seen material which quite matched the material from Ireland, the only European area where the species has been found. I am familiar with the Irish material only through collections from Lough Coomeathean and Lough Currane, Waterville, Ireland (E. W. Jones) a collection of G. A. Holt (Cromaglown, June, 1885), and through the figures of Macvicar. The Irish plant differs from the American in having even more oblong leaves than in such American plants as in Fig. XXVI: 3, and particularly in the narrower underleaves. The underleaves tend to be oval-oblong, as figured by Macvicar (1926), and as is emphasized in his text. Such prominently elongated underleaves simply fail to occur in our plants, in which they are always subrotund to broadly ovate. Macvicar also emphasizes as one of the distinctive features of the Irish plant the fact that the perianth is only *slightly and obtusely 5-angled* (italics his!). As Evans (1902) has emphasized, the American plant has sharply pentagonal perianths, whose keels are often narrowly winged! These differences suggest that the Irish plant belongs to a discrete race or subspecies, for which Lindberg's early name, *L. moorei*, may be used.

It is also reasonably certain, from the work of Eifrig (1937) and Greig-Smith (1948), that the division of the species into only two races would be an over-simplification, but I do not have available the material needed to study the species fully on a world-wide basis. Eifrig pointed out that the Indo-Malayan material, of which he examined ten collections, had a mean cell area of 232.7μ^2 (range: 185.8–273.6μ^2); the five specimens he studied from the West Indies showed a mean cell area of 295.6μ^2 (range: 270.9–319.7μ^2). From this he concluded that two discrete races were at hand, which he did not attempt to separate nomenclatorially, evidently because no obvious morphological characters were at hand to do so. Greig-Smith, using the same technique as Eifrig had used to insure that cells from mature leaves were studied, did not find such a clear geographical segregation into cell-size groups. Using submarginal apical cells, as did Eifrig, he obtained results at variance with those of Eifrig. The West Indian material showed cells varying from 246.9 to 229.3μ^2; the single South American plant gave a figure of 155.5μ^2. By contrast, Irish plants ranged from 188.0–237.9μ^2, and a collection from Madeira had cells of 213.0μ^2. An Australian specimen had cells of 171.0μ^2. Although the two sets of data show clearly that the cell sizes of the West Indian plants range at the upper end of the scale, and the material

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in certain respects. It evidently represents a saxicolous, xerophytic phase, bright yellow-green in color, rather dull, and rather opaque. The leaves of fertile shoots and branches are often provided with vestigial lobules. The cells often have more numerous (12–18), smaller, but distinctly segmented oil-bodies. In spite of these deviant features, these plants can only be considered to be a poorly developed extreme of the xeromorphic "*L. americana*" extreme of *L. flava*. Lobulate leaves of these plants show the typical, large lobules (*ca.* 0.35–0.4 times the length of lobe) of the "*L. americana*" extreme.

from Indo-Malaya and Australia had patently smaller cells, the cell size of the plants from the Oceanic Islands (Madeira to Ireland) were clearly intermediate. Further study of larger series is obviously desirable, and some effort should be made to correlate cell-size discrepancies with other morphological discrepancies, if such can be found. The writer would agree with Greig-Smith that *L. flava* is "an old species which has split up into numerous geographically isolated populations."

A comparison of limited Japanese material (which is presumably allied to the Indo-Malayan race) suggests other points of difference from those brought out by Eifrig, and corroborated to some extent by Greig-Smith. The cell size is admittedly somewhat smaller than in the New World race. I have used the marginal cells of the apical half of the lobe as a criterion, rather than submarginal, and tangential diameter rather than area, since these measurements are much more easily made. In American plants the marginal cells of the lobes of leaves of main stems average (rows of 6–7 cells) 16.0, 16.4, 16.9, 18.6, 19.1, 20.0μ (Louisiana, *Pennebaker, 1939*) or 17.1, 18.0, 18.5, 19.1, 20.0μ (Sanford, Fla., *Rapp, 1934*). By contrast, the Japanese plants (Hattori's Hep. Jap. *No. 135*) had the marginal cells 13.9, 14.6, 15.5, 17.0, 17.7, and 18.1μ when averaged in series of 6–7. In the American plants, the total average of 11 measurements is 18.2μ; in the Japanese, 6 measurements average out to 16.1μ. The Japanese plants, however, closely agree with American *L. flava* in the subrotund underleaves, closely matching, for example, Fig. XXVI: 4 and 11.

It is therefore apparent that three races of *L. flava* may be differentiated, at least on a tentative basis, as by the subjoined key:

a. Underleaves rotund-ovate, averaging on main shoots 0.95–1.15 times as broad as long, broadly rounded at base to distinctly cordate; leaves oblong-ovate to ovate; perianth sharply 5-carinate in distal half, the carinae often weakly winged ..... b.

b. Leaf cells averaging smaller: the marginal, 13.9–18.1μ, the subapical with area 185–275μ^2; underleaf bases commonly strongly cordate. Japan and Indo-Malaya.
L. flava subsp. *orientalis* subsp. n.[20]

b. Leaf cells averaging larger: the marginal, (16.0) 16.9–20.0μ, the subapical with area 245–320μ^2; underleaf bases usually weakly cordate. America.
L. flava subsp. *flava* (Sw.) Nees

a. Underleaves oblong-ovate, averaging 0.75–0.90 times as broad as long, narrowly rounded and not to weakly cordate at base; leaves narrowly oblong-ovate to elliptical-oblong; perianth slightly and obtusely 5-angled above; marginal leaf cells, near apices, 13.9–18.5μ. Ireland ..... *L. flava* subsp. *moorei* (Ldbg.) comb. n.[21]

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[20] Type: Hattori's *Hep. Jap. No. 135*, Miyazaki, Kiushiu, Japan (*Hattori*). *L. flava* subsp. *flava* peraffine. Differt cellulae marginalis 13.9–18.1μ; amphigastria subrotunda, basi leviter cordata, lobis late triangulatis.

[21] Type: Cromaglown, Ireland (*Holt*); *Lejeunea moorei* Lindberg, Acta Soc. Sci. Fenn. **10**: 487, 1875.

I have carefully checked mature plants of the two collections made by E. W. Jones near Waterville, Kerry, Ireland. In the plants from Lough Coomeathean the marginal cells average (rows of 6–8 cells) from 15.0–15.5–15.7–16.0–16.5–16.9–18.1–18.5μ; the underleaves range from 295 × 390μ to 360 × 410μ to 420 × 460μ long (0.76–0.91 times as broad as long) but are rather distinctly cordate at base. In the plants from Lough Currane the marginal

The above arrangements will probably have to be modified when more material becomes available. However, it must be pointed out that I have seen no American material with underleaves as strongly cordate at base as is the case in the Japanese plants; nor have I seen plants in which the cells average as small on the leaf-margins. Similarly, in the long series of American plants studied, I have seen none with the robust size, narrow lobes and narrow and elongate underleaves of the Irish plants. Future study, therefore, will surely be in the direction of recognition of more subspecies, rather than fewer, in this polymorphous complex. From the description of the underleaves ("width 70–85% of the length") I would judge that the South African material cited by Arnell (1953, p. 276) belongs to the subsp. *moorei*; the small lobule size ("surface $\frac{1}{30}$ of the surface of the lobe") also suggests such a disposition of the African plants.

Lejeunea (*Lejeunea*) *lamacerina* Gottsche ex Stephani

Lejeunea serpyllifolia forma *a planiuscula* Lindberg, Acta Soc. Sci. Fenn. **10**: 484, 1875.
Lejeunea cavifolia var. *planiuscula* Lindberg, Musci Scand. 2, 1879.
Lejeunea lamacerina G. ex Steph., Hedwigia **35**: 91, 1896; Stephani, Spec. Hep. **5**: 804, 1915; Persson, Bot. Notiser 1939, 566; Greig-Smith, Trans. Brit. Bryol. Soc. **2**(3): 459, figs. 3–4, 1954.
Lejeunea patens, in part, of American authors (including Evans, 1902; Blomquist, 1936; Sharp, 1939; Frye and Clark, 1947), and of Schuster and Hattori (1954).
Lejeunea cavifolia Macvicar, Studs. Hdb. Brit. Hep. Ed. II: 430, *pro max. parte* (*nec* Lindberg).
Lejeunea planiuscula Buch, Rev. Bryol. et Lichen. n.s. **7**(3–4): 243, figs. 1–2, 5, 11, 14, 1934.

Plants pale to whitish green, glistening when dry, loosely prostrate, 5–15 mm. long × (700) 850–1000μ wide, rather sparingly, irregularly branched; stems *ca.* 75–100μ in diam. Leaves *contiguous to weakly imbricate*, occasionally remote, *moderately* convex, obliquely spreading (55–70°), *broadly ovate to ovate-rotundate, hardly to barely falcate, widest slightly below the middle or at basal third*, the anterior margin erect and not expanded basally (extending to stem midline or barely beyond midline), but the *area above the narrow base rather strongly dilated* and then evenly arched outward to the *broadly rounded apex*; postical margin slightly convexly arched, *only weakly and obtusely notched at juncture with keel*; lobe *ca.* 400–440μ wide at basal third (maximal width) × 550–630μ long (from keel base) on mature shoots. Lobule strongly inflated, *relatively small* (area 0.08–0.2× that of lobe; 0.7–1.0× that of adjacent underleaves; length 0.25–0.35× that of lobe), *with moderately or weakly arched keel* which is nearly continuous with posterior lobe margin, its free, anterior margin involute basally but appressed to lobe at least distally, the *apical tooth straight, not incurved, blunt and rather short*; lobule *ca.* 190–210μ long × 130–160μ wide. Cells (15) 17–20 (22)μ on margins, as in subsp. *gemminata*, with few, segmented oil-bodies. *Underleaves remote*, subrotundate, to *ca.* 220–235μ wide × 180–225μ long, averaging as wide as or slightly wider than long, divided to within 3–4 cells of the small, inconspicuous rhizoid-initial region by a *very frequently U-shaped or lunate sinus*; lobes acute, terminated by 1–2 superimposed cells, often 5–6 cells wide at base, occasionally *with an obscure lateral angulation or tooth*.

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rows of cells average from 13.9–14.1–15.0–15.7–16.0–16.9μ; the underleaves range from 220μ wide × 270μ long up to 310 × 350μ or occasionally 380 × 400μ (0.82–0.95 as broad as long; rarely to 1.0 as broad as long). The marginal cells, therefore, are as in the subsp. *orientalis* and average somewhat smaller than in typical *L. flava*. More striking is the narrow leaf form! This ranges from 275 × 425μ to 280 × 420μ to 320 × 475μ up to 385 × 630μ; thus the lobes are 1.43–1.64 as long as wide, with length measured from base of keel (vs. 1.24–1.38 in *L. flava* subsp. *flava*). The few perianths seen are also clearly provided with weaker, shorter carinae!

Autoecious. Androecia small, inconspicuous, usually of 2-3 pairs of bracts, on short lateral branches that are leafless and do not proliferate, very rarely terminal on leafy shoots. Gynoecia usually on leading, leafy shoots, then *almost invariably with one innovation* (which may again be fertile) rarely with two, occasionally cladogynous *on usually leafy lateral branches* and with one innovation. Bracts variable: one of a pair often with lobe broad (*ca.* 270μ wide × 400μ long to 370–415 × 500–510μ long) and rotundate-obovate; lobule short and broad, rounded at apex (from 265μ long × 100μ broad to 235–360μ long × 85–100μ broad), the *lobule averaging 0.4–0.55 times the length of lobe*, free for up to half its length; other bract of a pair often narrower and elliptical to narrowly obovate, to obovate-lingulate, 475–540μ long × 235–335μ broad, the lobule from 210μ long × 85μ wide up to 175μ long × 70μ wide, *small and lingulate, averaging 0.4–0.45 times length of lobe*. Perianth obovoid-obpyriform, *sharply 5-carinate to within the perianth-middle, the keels high, entire to faintly crenulate*, the perianth not appearing strongly inflated.

TYPE: Azores.

DISTRIBUTION.—According to the literature, restricted to the oceanic and western portions of Europe, and the Atlantic Islands, but the range not fully elucidated, owing to confusion, until very recently, with *L. serpyllifolia* and *L. cavifolia*. Found from the Azores and Madeira, the Canary Islands, northward to n.w. Spain, s.w. France (Allorge, 1955) to western England, Ireland (Greig-Smith, 1954), northward to the Faroe Islands; also reported (Müller, 1954) from Baden, Germany.

The species has also been reported (subsequent to the completion of this treatment) from Newfoundland (Buch and Tuomikoski, 1955). It is presumed that this report refers to the nearctic subspecies, described below, although the material has not yet become available for study. In any case, no wholly typical material of *L. lamacerina* has been seen from North America.

The North American vicariant of *L. lamacerina* has been uniformly confused with *L. "patens"* (= *L. serpyllifolia*) in this country; this plant is here described as subsp. *gemminata* of *L. lamacerina*.

DIFFERENTIATION AND VARIATION.—*L. lamacerina* and *L. serpyllifolia* form an exceedingly difficult complex. The chief differential features are contrasted in the keys to species (pp. 142–150), and in Table I. Some of these features have been analyzed statistically by Greig-Smith (1954), using only European populations.

Although Greig-Smith was able to show conclusively that the two taxa were "good" species in Europe, study of the Appalachian material, which has been uniformly referred to *L. "patens"* (*L. serpyllifolia*) in North America since the time of Evans (1902), revealed that in some important respects the American plants showed variation from a *"lamacerina"* extreme to the *"serpyllifolia"* extreme. Indeed, desultory study of the problem, in the years 1950–56 failed to clarify the problem of the specific identity of the American plants. Before these American plants are treated in detail, it may be well to establish the criteria which appear to separate the two species in Europe, some of which are tabulated in Table I.

The two "typical" taxa, as found from the Azores to the Faroes and along the Atlantic coastline of Europe, differ primarily as follows: (a) *L. lamacerina* has small lobules, usually $\frac{1}{8}$–$\frac{1}{12}$ of the area of the lobes (Fig. XXVII: 1, 8–9, 12); *L. serpyllifolia* has large lobules, usually $\frac{1}{3}$–$\frac{1}{5}$ or up to $\frac{1}{8}$ of the area of the lobes (Fig. XXXII: 1–2, 4); (b) the lobes are broadly ovate and hardly

falcate in *L. lamacerina* (Fig. XXVII: 1, 8–9, 12); in *L. serpyllifolia* they are narrowly ovate, not strongly dilated above the antical base, but very strongly falcate (Fig. XXXII: 1–2, 4–5); (c) the postical leaf-margin is weakly notched, and the keel usually weakly arched, in *L. lamacerina*; in *L. serpyllifolia* the

TABLE I

Differential features of the L. lamacerina-L. serpyllifolia *complex*

	L. lamacerina	*L. lamacerina gemminata*	*L. serpyllifolia* (*L. patens*)
Lobe	Weakly falcate, broadly ovate, widest above base, broadly rounded.	Weakly to moderately falcate, broadly ovate, widest above base; ± narrowly rounded at apex.	Strongly falcate, narrowly ovate, widest near middle; broadly rounded at apex.
Lobule margin and apex	Free margin weakly involute distally; apical tooth blunt and short, straight.	Free margin weakly or sometimes strongly involute distally; apical tooth usually straight and blunt, occasionally longer and curved.	Free margin involute to and including the long, falcate apical tooth.
Notch at apex of keel	Very obtuse and usually shallow, 110–175°	Usually obtuse to rectangulate, 90°–145°	Usually sharp and deep, 75–100°
Lobule:lobe size ratio and length, on stem leaves	1:8–12 area; 1:2.5–3 length	1:(4)5–15 area; 1:2–3 length	1:3–5(8) area; 1:1.8–2.2 length
Underleaves: sinus and size	Often with broadly lunate sinus; larger than lobules.	Sinus usually narrow, occasionally narrowly lunate, rarely broadly lunate; 0.8–1.5× as large as lobules.	Sinus narrow, ? never lunate; 0.8–1.0× as large as lobules.
Bract lobes	Broadly obovate, at least in part	Narrowly ovate to obovate	Narrowly ovate to obovate
Bract lobules	Short, broad, blunt: length *ca.* 0.4–0.5× lobe length, in large part.	Lingulate, blunt, 0.55–0.8× length of lobe.	Lingulate, subacute to blunt, 0.55–0.7× length of lobe
Gynoecia	Often acrogynous; but with 1 innovation, rarely 2.	Often acrogynous, then usually with 2 innovations.	Most often cladogynous, 1 innovation, rarely 2.
Perianth keels	Sharp, descending *ca.* 0.5–0.7.	Usually low, descending 0.35–0.45, never winged or denticulate.	Sharp, descending 0.5–0.6 at least, often denticulate.
Cells on margins	(14.5)16–20(22)μ	(18)19–21(22–23)μ	(13.9)14.5–18.5(19.2)μ
Median cells	Trigones weak to absent; usually without intermediate thickenings.	Trigones weak to (rarely) salient; intermediate thickenings absent to (rarely) obvious.	Usually with distinct trigones and intermediate thickenings, rarely almost absent.

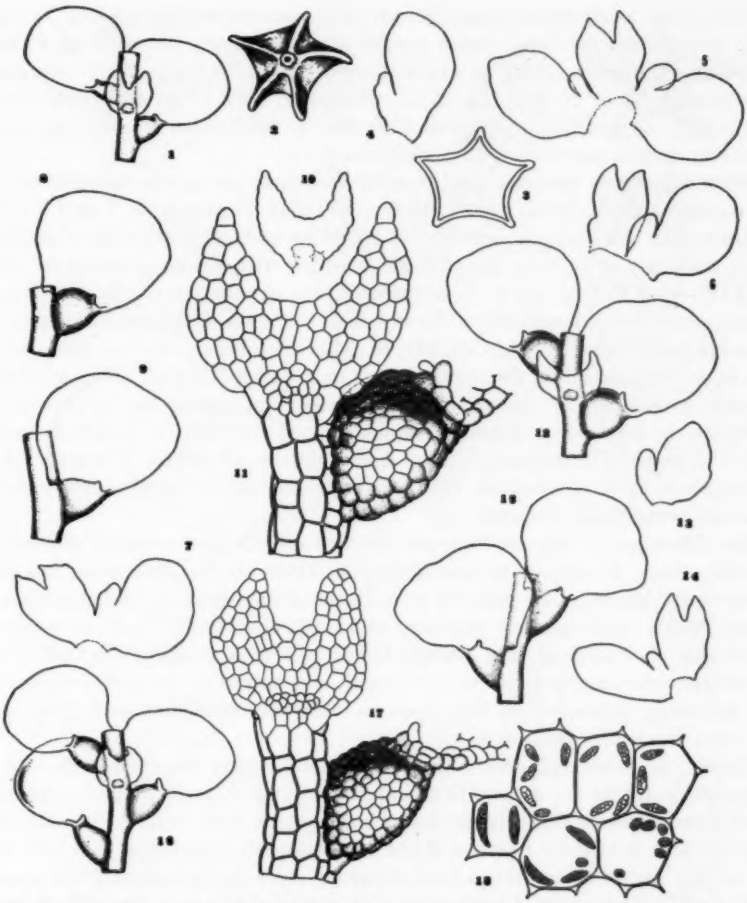

FIG. XXVII. *Lejeunea lamacerina* subsp. *lamacerina* G. ex Steph. 1. Part of shoot, postical aspect, from leading stem (×30); 2–3. Cross-sections of perianth, 2 at apex, 3, one-fourth from tip (×42); 4. Bract (×30); 5. Bracts and bracteole (×30); 6. Bract and bracteole (×33); 7. Bracts and bracteole (×33); 8–9. Leaves, dorsal view, *in situ* (×33); 10. Underleaf (×65); 11. Underleaf and lobule, *in situ* (×138); 12. Shoot-sector, postical aspect (×42); 13–14. Bracts and bracteole from one gynoecium (×33). *L. lamacerina* subsp. *gemminata* Schust. 15. Robust shoot sector, antical view (×32); 16. Shoot sector, postical view (×32); 17. Underleaf and lobule, *in situ* (×100); 18. Median cells with oil-bodies (×415). (Figs. 1–5 from a specimen collected by A. C. Crundwell at Campsie Glen, Stirlingshire, Scotland, as "*L. patens*;" 6–14, from Verdoorn, Hep. Sel. et Crit. 420, Cornwall, England; 15–18, from *Schuster 28882*, Linville Gorge, N. C.)

postical leaf-margin is sharply incised, and the keel below strongly arched; (d) trigones are small or vestigial, and intermediate thickenings usually absent, although occasionally distinct, in *L. lamacerina*; these are usually strongly developed in *L. serpyllifolia*; (e) the free lobular margin is less strongly involute,

and the apical tooth distinct, not curved, in *L. lamacerina* (Fig. XXVII: 11–12); in *L. serpyllifolia* the free lobular margin is very strongly involute, up to and including the falcate, elongate apical tooth (Fig. XXXII: 2–4); (f) marginal cells usually (14.5) 16–20 (22)μ in *L. lamacerina*; only (13.9) 14.5–15.8 (18.6–19.2)μ in *L. serpyllifolia*; associated with this, *L. lamacerina* is usually a paler, more transparent plant than *L. serpyllifolia*.

Other differences between the two taxa exist that are hardly brought out in the papers of Buch (1934) and Greig-Smith (1954). For example, I find that in *L. lamacerina* the gynoecia are often acrogynous and, in the American populations, are often or at least sporadically provided with paired innovations (Fig. XXVIII: 4; XXIX: 5–6); in *L. serpyllifolia* the gynoecia are typically almost all on more or less strongly abbreviated lateral branches, and gemminate innovations are rare or absent (Fig. XXXII: 6). This distinction, which appears to be real, is not brought out in the treatment of Greig-Smith (1954). A sharp tendency towards production of paired innovations does not appear to be present in European *L. lamacerina*, although frequently well expressed in American material. Yet even in European, typical *L. lamacerina* (Scotland: Campsie Glen, Stirlingshire, A. C. Crundwell, 1950; as "*Lejeunea patens*") gemminate innovations are occasionally frequent.

The difference in cell size between the two species, like all other differences between them, is subject to intergradation. However, *L. lamacerina* has preponderantly larger, more pellucid cells, those of the margins averaging usually about 18–20μ, with sporadic extremes of 14–16μ and 20–22μ; in *L. serpyllifolia* I find that the marginal cells average (13.9) 14.5–15.5, rarely up to 18.6–19.2μ. These distinctions appear to be quite valid, and appear to be crucial in placing the American plants, which have been so uniformly misunderstood; they have not been utilized by Greig-Smith.[22]

Finally, *L. lamacerina* has a basically different lobe shape from that of *L. serpyllifolia*. In the first, the antical margin is asymmetrically arched, appearing much more dilated a short distance above the antical base, with the consequence that the lobe is broadly ovate in shape and relatively broad (Fig. XXVII: 8–9, 12, 15–16). In the latter, the antical margin is more evenly arched from base to apex, and not strongly dilated, with the consequence that the lobe is more nearly elliptical, disregarding the falcate form and area lying over the lobule (Fig. XXXII: 1, 5). This feature will be treated again later.

In spite of the range of characters that can be utilized to separate *L. lamacerina* from *L. serpyllifolia*, it must be admitted, with Greig-Smith (*l.c.*): "that no character given is invariable in any of the species." Therefore, occasional individuals will be found, the disposition of which can only remain in doubt.

This doubt is particularly great when it comes to a study of the American

[22] Buch (1934) does not appear to have studied his material critically, or else his plants were transitional in this respect. He stated that in "*L. patens*" (*L. serpyllifolia*) the marginal cells were 14–20μ, and that in "*L. planiuscula*" (*L. lamacerina*) they were 14–19μ! Table I appears to show that such a virtual identity in cell size does not exist. Indeed, in the case of "moot" materials, cell size may be the final criterion for effecting a separation.

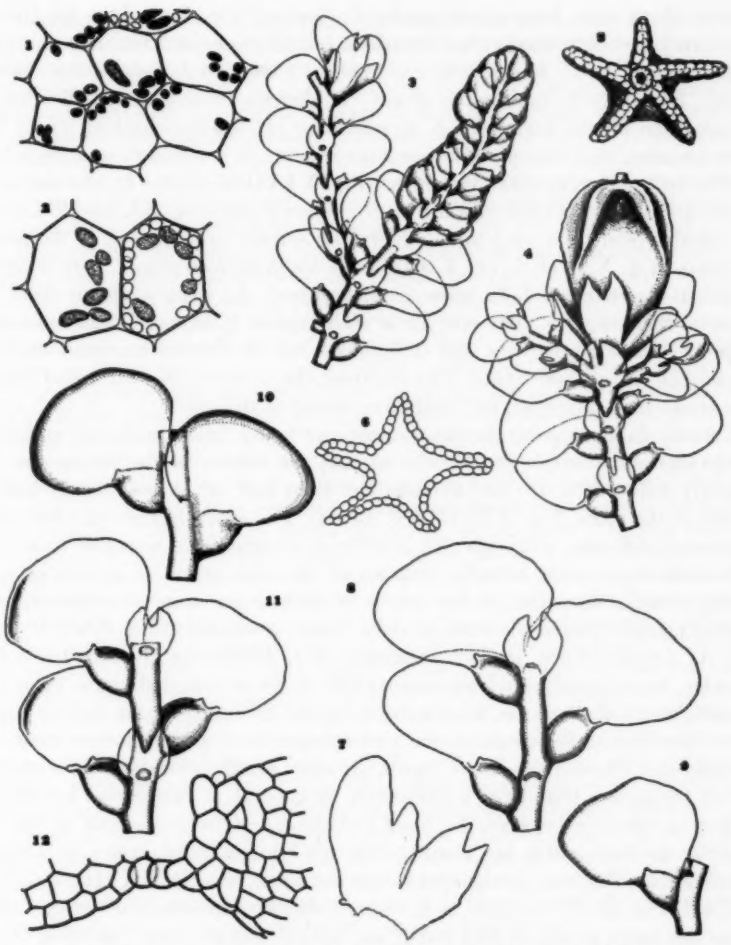

FIG. XXVIII. *Lejeunea lamacerina* subsp. *gemminata* Schust., showing gradation to subsp. *lamacerina* in perianth form and lobule size. 1. Median cells with oil-bodies (×400); 2. Median cells with oil-bodies and chloroplasts (×640); 3. Shoot apex, with elongate cladogynous branch and acrogenous androecium (×27); 4. Shoot apex with acrogynous gynoecium and gemminate innovations (×37); 5–6. Perianth cross-section at 5 at apex, at 6 one-fourth the distance below apex (×73); 7. Bract and bracteole (×39); 8. Shoot-sector of plant of maximal size, 1215μ wide, postical aspect (×40); 9. Leaf, *in situ*, dorsal view (×40); 10. Two leaves, *in situ*, dorsal view (×48); 11. Shoot-sector, postical view (×48); 12. Apex of lobule, hardly flattened (×174). (1 from *RMS 18301*, W. Virginia; 2–9, *RMS 37968*, Roan Mt., Tenn.; 10–12, Whitewater R. Gorge, N. C., *RMS 25014a*.)

plants, which have been placed under *L. "patens"* by all workers for the last fifty-five years. Admittedly, the American plants show some features that place them "closer" to *L. serpyllifolia* (*L. "patens"*) than to *L. lamacerina*. For example, European *L. lamacerina* shows "tendencies" which set it off from the Appalachian plants, and from *L. serpyllifolia:* (a) the perichaetial bracts tend to be broader, with broadly obovate lobes frequently developed, and the lobules tend to be small, very short and broad (Fig. XXVII: 4–6, 13–14); (b) the underleaves are often provided with a broadly lunate sinus (Fig. XXVII: 10–12); (c) the lobules tend to be very small, averaging usually only $\frac{1}{8}$–$\frac{1}{15}$ of the area of the lobes (Fig. XXVII: 1, 12). Even though the American plants, here separated as subsp. *gemminata* of *L. lamacerina*, approach *L. serpyllifolia* in these and certain other respects, they still agree with typical *L. lamacerina* in most other respects. These similarities and differences will be treated in detail under *L. lamacerina* subsp. *gemminata*. Two features, the form of the bracts and the leaf lobe shape may, however, be briefly mentioned at this point.

Typical *L. lamacerina* deviates quite markedly from both the subspecies *gemminata* and from *L. serpyllifolia* in that the lobules of the bracts are often strongly reduced in size and average less than half, or at best barely half the length of the lobes (Fig. XXVII: 4–6, 13–14). The shape of the leaf lobes is also somewhat different, although this is difficult to express in accurate terms. The lobe tends to be more broadly rounded at the apex (as in *L. serpyllifolia*, but unlike subsp. *gemminata*); it has nearly or quite as pronounced a dilation of the antical margin, above the base, as does subsp. *gemminata* (Fig. XXVII: 1, 8–9, 12). As a consequence, in both subspecies of *L. lamacerina* the lobe tends to be broader, more broadly and asymmetrically ovate or rounded-ovate than in *L. serpyllifolia*, but the lobe, associated with the less arched and shorter keel, is much less distinctly falcate in the two subspecies of *L. lamacerina* than in *L. serpyllifolia*. These distinctions, again, are more readily evident from a comparison of the figures than from a discussion. In general, *L. lamacerina* has the lobe widest in the area between the basal one-third and basal one-half of the lobe, and the greatest width lies along a line (*a'*) lying at right angles to a line (*a*) running from the base of the keel to the leaf apex; see Fig. XXVII: 8–9, 15 and XXXII: 1, 5, 12. By contrast, in *L. serpyllifolia* the narrower and strongly falcate lobes are more evenly arched along the antical margin, and (omitting the depressed lobar area lying over the lobule) are widest near the middle, along a line (*b'*), lying at nearly right angles to a line (*b*) running from antical leaf base to leaf apex.

Lejeunea lamacerina subsp. **gemminata** subsp. n.

L. lamacerinae formae typicae similis sed differt foliis distinctius ovatis et obtusis; lobulis plerumque grandioribus et magis inflatis, saepe dente apicali praeditis; gynoeciis saepe terminalibus in novellis longis et innovationes duas ferentibus; perianthiis subcostatis, costis saepe indistinctis, aspectu valde inflatis. Specimen typicum legit R. M. Schuster, no. 36621, monte "Andrews Bald," prope "Clingmans Dome, Swain Co." in Carolina Septentrionali.

In thin, whitish to pale yellowish-green patches, or scattered, on rocks or on

bark, weakly to distinctly shiny when dry. Plants loosely prostrate, 5–12 mm. long × (650–750) 820–1050 (1150–1215)μ wide, irregularly and rather freely branched; rhizoids scarce to rather numerous, but in only small, inconspicuous initial regions; stem 75–90μ in diam.; ventral cortical cells mostly (23) 25–30 (32)μ broad. Leaves of stems subimbricate to weakly imbricate, *leaving the dorsal stem surface at least slightly exposed*, obliquely spreading (45–65°), *somewhat to markedly convex* when dry, broadly and asymmetrically ovate to ovate-rotundate, *little to moderately falcate*, 350–435 (520)μ long from keel to the *usually narrowly rounded, deflexed apex* × 320–400μ wide from postical incision to widest point of lobe, occasionally up to 600–630 (670)μ long × (470) 510–520μ wide in robust forms of moist shaded ground (then only weakly convex and with unusually small lobules); width usually 0.75–0.90× the length; antical margin nearly straight, not curved initially, lying nearly parallel with stem, then abruptly and strongly arched, thus appearing *very strongly dilated above the strongly narrowed base, the widest point lying about 0.25–0.35 of length above base*, with greatest width (measured from notch at apex of keel) in a line at right angles to a line running from base of keel to lobe apex; antical leaf-margin, above the narrow base, usually so strongly dilated that it extends *partly or wholly across the stem*, then gradually and evenly arched outward to the usually *relatively narrowly rounded apex* which is commonly somewhat deflexed; postical margin evenly and usually more weakly rounded, from apex of keel, to the apex of lobe; *keel strongly arched and at its apex strongly incised* (incision 80–100°) in xeromorphic forms, much less weakly incised (110–170°) in mesic extremes, which have reduced lobules. Lobule strongly inflated, its free margin involute at base, but often *flatly appressed to lobe distally* (in extreme xeromorphic forms with very convex lobes this often not clear without artificially flattening leaves), the *apical tooth usually short and blunt, not or hardly curved* (rarely elongate); *lobule averaging 0.1–0.25 times the area of lobe, its length 0.35–0.45 (0.5) times that of lobe, ca.* (150–190) 200–260μ long × (100) 135–150μ broad. Cells usually thin-walled and with small to moderately small trigones, with intermediate thickenings few and weak or none; marginal cells (18.0) 18.6–22.0 (23.0)μ, median cells from (19–21) 22–25 (27) × (22) 23–28 (30)μ; *oil-bodies few per cell*, usually (2) 3–6 (8) per cell, spherical and short-ovoid and 2.5–3 × 3–4μ to 3.5–4 × 6–7μ, often ellipsoidal and 3.2–4 × 8–11μ up to 4.5 × 10μ, *finely segmented*, larger than chloroplasts (which are up to 4μ). Underleaves varying considerably, usually subrotundate and 140–165μ wide and long to ovate and 220μ wide × 235μ long to broadly rotundate and 220–225μ wide × 180–215 (235)μ long, averaging 2.0–2.5 times as wide as stem, with sinus acute and *narrowly open to U-shaped, rarely broadly lunate*, descending to within 3–4 cells of the small rhizoid-initial region; *underleaf area usually subequal to lobule area, occasionally slightly greater*.

Autoecious. Androecia commonly small, of 3–4 pairs of bracts, forming small lateral branches, devoid of leaves and proliferating apically, forming spikes 320–350μ wide, less often of 8–12 pairs of bracts and distinctly spicate, rarely spicate and intercalary on leafy shoots. Gynoecia in large part terminal on long, leafy shoots, with *occasionally to usually 2 innovations*, which may be again floriferous (but then bear single innovations); *cladogynous gynoecia usually rather infrequent*, sometimes nearly or quite lacking. Bracts averaging slightly smaller than adjacent leaves or subequal in length, the *lobes narrowly obovoid to lingulate*, (470–480) 530–570μ long × (210–230) 270–325μ broad; lobules *ca.* 290–350 (430–450)μ long × (75) 80–120μ broad, lingulate, blunt to rounded at apex, free for distal 0.2–0.3, *their length 0.55–0.75 times that of lobes*. Bracteole oblong-elliptical, 340–460μ long × 175–250μ broad, united for 0.1–0.2 of its length with one or both bracts, *bifid 0.2–0.3 its length*, the sinus more or less acute, the lobes acute. Perianths 0.4–0.5 emergent, narrowly obovoid, strongly

inflated, *weakly to moderately 5-carinate in the distal 0.3–0.5*, 360–470μ wide × 720–760 (820)μ long; carinae smooth or weakly crenulate, often low and inconspicuous.

TYPE: Andrews Bald, *ca.* 4700 ft., s. of Clingmans Dome, Smoky Mts. National Park, Swain Co., North Carolina (*RMS 36621*); type in collection of author (at University of Michigan) and in herb. Duke University. The diagnosis prepared from the type, and from an isotype (*RMS 36608*).[23]

DISTRIBUTION.—Appalachian in range, occurring southward from northern Georgia, North Carolina, and Tennessee, northward to New England and Nova Scotia and presumably Newfoundland; northward, becoming restricted to the extreme east, but descending to sea-level; southward, restricted to the Southern Appalachians, not found below 1800–2500 ft., and rare at such elevations, although ascending to 5700–6680 ft.

The distribution of this plant is still very poorly known because of (a) the uniform confusion, previously, with "*Lejeunea patens*" (= *L. serpyllifolia*), and in some cases with *L. cavifolia*; (b) the difficulty in surely effecting a separation between this plant and between typical *L. lamacerina*, on one hand, and *L. serpyllifolia*, on the other. Presumably *L. serpyllifolia* is absent from North America, although there are numerous reports (compiled under that species; see p. 186).

CANADA. **Newfoundland:** Biscay Bay, Avalon Distr.; Pass Isl., S. Coast; Benoit Brook, W. Nfld. (Buch & Tuomikoski, 1955; as *L. lamacerina*). Although I have not seen the specimens upon which this report is based, I presume that the American race is involved. **Nova Scotia:** Sandy Cove, Digby (*M. S. Brown, 1936*); this is one of the specimens reported as "*L. patens*" from Nova Scotia by Brown (1936). The specimen clearly belongs here, on the basis of the large cells (19–24μ on the lobe margins), the almost wholly acrogynous inflorescences, partly with 2 innovations, as in *L. lamacerina*, but with the large lobules, with a "*patens*-type" apical tooth, as in subsp. *gemminata*.

UNITED STATES. **Virginia:** GILES CO. (Garden of the Gods, Mountain Lake, *Sharp 3996*); SMYTH CO. (White Top Mt., at 4000–4500 ft., *Schuster and Patterson 38050b, 38054a, 38087, 38095*); RAPPAHANNOCK CO. (Buck Hollow Trail, 1500–3000 ft., *Schnooberger 4538;* gynoecia all on leading shoots, with 1 innovation). **West Virginia:** PENDLETON CO. (W. of Mouth of Seneca, Seneca Rocks, Monongahala Ntl. Forest, *RMS 18301* (plate)). **North Carolina:** SWAIN CO. (Andrews Bald, *ca.* 5700 ft., s. of Clingmans Dome, *RMS 36621*, type and *36609*, isotype (plate), *RMS 36608*, isotype (plate); Clingmans Dome, *ca.* 6200 ft., *RMS 36658, 28106;* in *28106* with gynoecia usually but not always acrogynous, often with 2 innovations; lobules clearly of "*patens*-type," but with short apical tooth); BUNCOMBE CO. (Balsam Gap, 5260 ft., on Blue Ridge Parkway, *ca.* 25 mi. n.e. of Asheville, *RMS 19074a* (plate)); MITCHELL CO. (Roan Mt., near Tennessee border, at *ca.* 6100 ft., *RMS 36962, 37968* (plate); a typical phase, with strongly ovate-narrowed lobes, rather small lobules, gynoecia of leading shoots most often with paired innovations and androecia often with 8–12 pairs of bracts, longly

[23] The material of these collections is used as the type, since it shows the most typical and most extreme expression of the features assigned to the subsp. *gemminata*, viz., frequent gemminate innovations; few or no cladogynous inflorescences; inflated and obsoletely quinquecarinate perianths; large leaf cells, etc. In the majority of other collections assigned to this taxon, these expressions are not uniformly present. For example, the almost eplicate, inflated perianths reappear in material from Tennessee (Cocke Co., *Sharp 39172*). Yet these plants have the gynoecia largely on short, lateral branches, while the few acrogynous inflorescences bear single innovations!

spicate; *RMS 36989a, p.p.*, among *Plagiochila tridenticulata*); JACKSON CO. (Whitewater R. Gorge, below High Falls, *RMS 25008, p.p., 25014a* (plate), *25018a;* Soco Falls, east of Cherokee, *RMS 24616, 24798, 3665a;* in *3665a* quite typical, with gynoecia acrogynous, but rarely with 2 innovations, never cladogynous); ASHE CO. (Nigger Mt., near Jefferson, *ca.* 4200 ft., *RMS 29623;* Bluff Mt., near W. Jefferson, *ca.* 4600 ft., *RMS 30059, 30055;* in *30055* typical, usually acrogynous but not wholly so, with 1 or 2 innovations); BURKE CO. (Linville Gorge, below Linville Falls, *ca.* 2500 ft., *RMS 26469, p.p., 28882* (plate); phase with wholly acrogynous gynoecia, usually with 1, sometimes with 2 innovations; *RMS 29461* (plate), typical phase with obtusely pentagonal perianth, partly gemminate innovations, but with frequently cladogynous inflorescences); CALDWELL CO. (near summit of Grandfather Mt., *ca.* 5800 ft., *RMS 30183c* (plate); a "*L. patens*" extreme, with very large trigones and large, "*patens*-type" lobules, but with acrogynous inflorescences, partly gemminate innovations, and large cells); MACON CO. (Dry Falls, near Highlands, Cullasaja Valley, *Blomquist 34638);* TRANSYLVANIA CO. (Whitewater R. Gorge, east side, below High Falls, 2500 ft., *RMS 25004, 25004a, p.p.*, among *Plagiochila sharpii* and *P. caduciloba);* YANCEY CO. (Summit of Mt. Mitchell, 6684 ft., *Anderson and Jones 9743, p.p.*, among *Plagiochila sullivantii*). **Tennessee:** SEVIER CO. (above Chimneys Parking Area, along branch of W. Fork of Little Pigeon R., 4500 ft., Smoky Mts., *RMS 36532b, 36534a;* Pinnacle near Greenbrier, 4000 ft., *Sharp 34574, 34577*, depauperate phase; Left Fork, Greenbrier, 3000 ft., *Sharp 3866a;* above Alum Cave Parking Lot, foot of Mt. Leconte, 4000 ft., *Sharp 5143);* BLOUNT CO. (Creek from Spruce Flat, *ca.* 1800 ft., above Middle Prong of Little R., below Tremont, *Schuster and Sharp 34621a;* Abrams Falls, Cades Cove, *Sharp 34725*, a phase with numerous gemminate innovations); CARTER CO. (near summit of S.W. peak of Roan Mt., 6100 ft., *RMS 37969*, among *Plagiochila tridenticulata);* COCKE CO. (near White Rocks, on exposed conglomerate, *Sharp 39172*, among *Plagiochila sullivantii;* a phase with inflated, weakly pentagonal perianths, but largely cladogynous inflorescences); MONROE CO. (Unicoi Mts., 3980 ft., Oak Lick Gap, Sassafras Ridge Rd., *Clebsch U-15);* the Tennessee material, other than that collected by the writer, forms the basis for the reports of "*L. patens*" from Tennessee in Sharp (1939) and Clebsch (1954). **Georgia:** TOWNS CO. (Brasstown Bald, 3500–4000 ft. and 4500 ft.; *RMS 34334, 34336a, 34347, 34311; 34347* almost exclusively with acrogynous gynoecia, most often with 2 innovations, but with "*patens*-type" lobule and underleaf).

The above all represent examinations of materials. The reports of "*Lejeunea patens*" from Newfoundland (Evans, 1902), Nova Scotia (Evans, 1902; Brown, 1936), Maine (Lorenz, 1924), Connecticut (Frye and Clark, 1947), Ohio (Conklin, 1926), Virginia (Patterson, 1949), West Virginia (Ammons, 1940) and Kentucky (Fulford, 1936) probably all should be referred to the present taxon. The report of "*L. patens*" from northern Georgia (Parker, 1941) needs verification. Of the material cited as "*L. patens*" from Virginia, by Schnooberger and Wynne (1945), two specimens have been studied. One, cited above, is *L. lamacerina gemminata*; the other (Little Devil Stairs, Rappahannock Co.) represents a misdetermination for *L. cavifolia.*

ECOLOGY.—*L. lamacerina gemminata* occurs both on damp to almost dry, shaded rocks, and on the bark of trees. It is corticolous only in humid areas.

The species is not infrequent at rather high elevations (5260–6200 ft.) in the Southern Appalachians, occurring on shaded damp rock-walls, usually in the shade of Spruce and Fir, and of *Rhododendron catawbiense*, associated with *Metzgeria fruticulosa, Herberta hutchinsiae tenuis, Radula tenax, Scapania nemorosa, Thuyidium delicatulum, Sematophyllum adnatum, Plagiochila sullivantii, P. tridenticulata, Tritomaria exsecta* and rarely, *Cephaloziella* (*Cephaloziop-*

sis) *pearsoni*. More rarely the plant is found, in such situations, on damp bark, associated occasionally with *Harpalejeunea ovata*, *Lejeunea ruthii* and *ulicina* and *Metzgeria fruticulosa*; it is almost always found on the bark of *Abies fraseri* in such situations.

The species is perhaps commoner at lower elevations in the Southern Appalachians, ranging from 2500–4200 ft. There it is found largely in the gorges and coves, associated with Mixed Mesophytic Forest and the Hemlock-Hardwoods Forest, usually on rocks, associated with: *Radula obconica*, *Leucolejeunea clypeata*, *Plagiochila caduciloba*, *P. sharpii*, *Harpalejeunea ovata*, *Lejeunea ruthii* etc., in less humid sites; in very damp sites, *Metzgeria hamata*, *Jubula pennsylvanica*, *Scapania nemorosa*, *Herberta*, *Radula tenax*, *R. sullivantii*, *Marsupella paroica*, etc. are usually associated. The plant occurs only rarely on bark at lower elevations (then in unusually humid sites; at times with *Metzgeria hamata* and *Radula tenax*, at other times alone on the branches of *Rhododendron maximum*). Occasionally persisting on rocks, at lower elevations, until thin soil-layers accumulate, then with *Plagiochila austini*, *Microlepidozia sylvatica* and *Diplophyllum apiculatum*, etc., but usually strictly a pioneer species. At the southern extreme of its range, in Georgia, occasionally on damp shaded rocks near stream margins; then with *Cephalozia media*, *Calypogeia muelleriana*, *Scapania nemorosa* and *Diplophyllum apiculatum*. In the same area, in Oak-Hickory Forest, also on bark of *Castanea dentata*, with *Frullania asagrayana*, *Lejeunea ulicina*, *Harpalejeunea*, *Radula obconica*, *Metzgeria crassipilis* and *furcata*.

Southward rarely occurring below 2500 ft., but found in Blount Co., Tennessee, down to 1800 ft., on damp vertical rocks near waterfalls, associated with *Lejeunea laetevirens*, *Plagiochila austini*, and *P. caduciloba*.

I have had no field experience with the species northward, where it is much rarer and more restricted in occurrence. Buch & Tuomikoski (1955), however, report it for Newfoundland from "sheltered clefts in rock walls," associated with *Blepharostoma trichophyllum*, *Scapania nemorosa* and *Eremonotus* (*Sphenolobus*) *minutus*. Such occurrences are identical with those characteristic of the species at high elevations in the Southern Appalachians.

DIFFERENTIATION.—This taxon is closely allied in many respects to the oceanic, European *L. lamacerina*, from which it differs chiefly in the following points: (a) perianths usually very weakly quinquecarinate, and only in the distal 0.3–0.4 (Fig. XXIX: 1–6); (b) the initial gynoecia terminal on the leading stems, subtended in some or most cases by gemminate innovations which are soon fertile (Fig. XXVIII: 4; XXIX: 5–6); (c) the lobule generally much as in *L. lamacerina*, that is, rather small and with the keel moderately arched and lobule moderately inflated, but often markedly larger (Fig. XXIX: 7, 12) and with (d) the apical tooth sometimes, although hardly commonly, elongated and curved, and approaching that of *L. serpyllifolia* (*L. "patens."*) (Fig. XXXI: 6–7, 12–13).

Although this plant has been uniformly called *L. "patens"* in the American literature, from the time of Evans (1902), "normal" manifestations are hardly to be confused with typical *L. serpyllifolia* (*L. "patens"*) a taxon with freely cladogynous inflorescences and usually with solitary innovations; with strongly

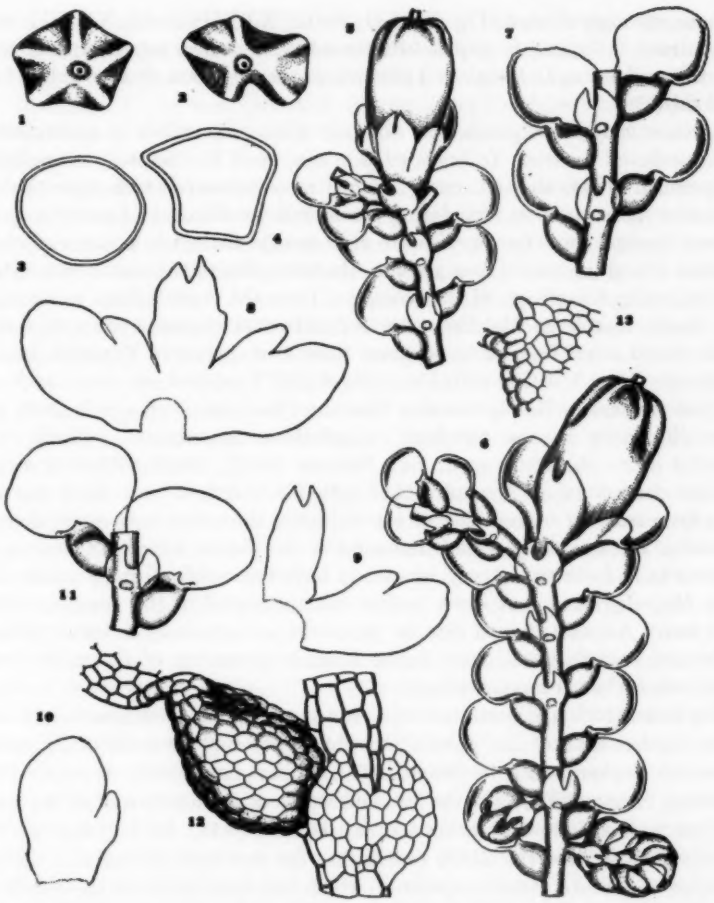

FIG. XXIX. *Lejeunea lamacerina* subsp. *gemminata* Schust., Type. 1, 2. Apices of perianths (×43); 3–4. Cross-sections through, respectively, middle, and distal one-third of perianth (×43); 5. Apex of rather slender plant, with 2 subfloral innovations, showing strongly inflated perianth (×33); 6. Basal and distal portions of robust plant, with intermediate portions omitted, with 1 subfloral innovation (×33); 7. Shoot-sector, postical aspect, not flattened, of extreme with large lobules (×44); 8–10. Two rings of bracts with bracteoles (×44); 11. Shoot-sector postical aspect, somewhat flattened (×44); 12. Lobule and underleaf, *in situ* (×127); 13. Flattened apex of lobule (×127). (All from the type, *Schuster 36621*.)

inflated lobules whose strongly involute free margin bears an elongated, somewhat curved, apical tooth; with the leaves more strongly convex, and with a nearly evenly arched antical leaf-margin (Fig. XXXII: 1–6). There is a marked tendency, in *L. lamacerina gemminata*, to have the antical leaf-margin, above

the base, strongly dilated (Fig. XXXII: 10–12; XXVII: 15–16; XXVIII: 8–11). By contrast, in typical *L. serpyllifolia* the lobes, in antical aspect, appear widest near the middle; in *L. lamacerina gemminata* the lobes are clearly widest in the basal third.[24]

Lejeunea lamacerina gemminata occupies a position which is uncomfortably "intermediate" between *L. lamacerina* s. str., and *L. "patens"* (*serpyllifolia*). Greig-Smith (1954) showed, using a much more advanced technique than had heretofore been used in elucidating taxonomic problems in *Lejeunea*, that in western Europe these two species are abundantly distinct in a series of characteristics. Using the conclusions given in the Greig-Smith treatment as a criterion for evaluating the plants of this complex, from the Appalachian mountains, I was wholly unable to find the same correlation of characteristics that Greig-Smith found could be used to separate these two species in England. In correspondence (Dec. 1, 1955) with Dr. Greig-Smith I pointed out that "as is often the case we find in North America that the "European" species behave somewhat differently in the Southern Appalachian mountains . . . Much of the material [from the latter area, *i.a.*, *Schuster 36608*, *36621*, *36532*] has 'intermediate characters' . . . I suspect that with the length of time these segregates have been isolated on our side of the Atlantic, there has been some divergent evolution. For one thing, I find that some of our plants, which fall close in most respects to *L. lamacerina*, very commonly have two subfloral innovations (much as in *Hygrolejeunea*—but quite unlike other material of the complex which I have seen). Associated with this the perianths are unusually inflated, with very slight and smooth keels, very unlike English specimens of *L. patens* (and *L. lamacerina*) which I have studied."

The basis which had been used to assign these Appalachian plants to *L. lamacerina* (rather than to *L. "patens,"* to which they had been uniformly assigned by recent workers, such as Sharp (1939), Blomquist (1936), Ammons (1940), following Evans (1902), was the size and shape of the lobule and of the apex of the lobule. (See following discussion and Buch (1934).) Buch (1934) first used criteria derived from the lobule to separate the two taxa, as well as a difference in shape of the lobe. Another criterion which had been used was the relative size of the lobule (as related to lobe and/or underleaf area), as in Buch (1934), etc. As I stated in correspondence to Greig-Smith, "I . . . find that there appears to be [in American plants] considerable variation in size of the lobule associated with environmental differences."[25] "In fact, I wonder if we are not relying too

[24] These measurements stand in contradiction to those given by Buch (1934), who stated that *L. lamacerina* (= *L. planiuscula*) had the lobes widest medially, and *L. patens* (= *L. serpyllifolia*) had the lobes widest in the basal third. I cannot confirm the observations of Buch. It will be noted that the material of *L. "patens"* from the type area in Ireland, possesses leaf lobes in which the greatest width is approximately at the end of the keel of the leaf.

[25] The lack of reliability of the association of lobule size and lobule apex, as related to lobe size, seems clear from material from the Southern Appalachians, from a deep spruce forest (*Shuster 19074a*). The mature plants of this number have very small lobules, a moderately arcuate keel, as in *L. lamacerina*, but often the long, curved apical tooth of *L. patens*!

As an added complexity might be cited a further specimen, from a Hemlock-Hardwoods

much on vegetative differences" (in separating *L. patens* and *L. lamacerina*). Buch (1934) "illustrates the cell of *lamacerina* as with trigones and intermediate thickenings, while you [i.e., Greig-Smith, 1954] assign the species leptodermous cells. Inversely, I find that typical *L. patens* (from the type locality; issued in Schiffner Hep. Eur. Exs. No. 1067) is quite leptodermous. I wonder if trigone development is not merely a reflection of the habitat."

At that time I also pointed out that European *L. "patens"* often has cladogynous inflorescences (Fig. XXXII: 6), rather infrequently acrogynous ones; *L. lamacerina* was more variable in this respect. In neither of these taxa, as occurring in Europe, did paired innovations occur in numbers, in the material available for study. By contrast, in Southern Appalachian material of this complex (e.g. in *Schuster 36608, 36621, 38087*) the first perianth produced is on an elongated leafy branch, which may bear one (Fig. XXIX: 6; XXX: 6) or often two innovations (Fig. XXVIII: 4), one or both of which may be fertile again. I then suggested, in correspondence with Greig-Smith, that possibly the "high incidence of gemminate innovations" might "warrant placing this as a separate var. *gemminata*."

As was noted in my letter to Greig-Smith, these illustrations showing discrepancies between the American plants and the European *L. lamacerina* and *L. "patens"* could be continued "ad infinitum: the main point appears to be that, in American plants, we do not find the same correlation of characters as in British material" (which was subjected to such a rigorous analysis in the paper by Greig-Smith, *l.c.*).

Greig-Smith (personal communication, Jan. 13, 1956) essentially corroborated the above observations, stating: "It seems clear to me that your plants belong to the same complex (i.e., the *L. patens-lamacerina* complex) but there is quite a different association of characters. In particular, a postical lobe shape of the *"patens"* type seems to occur with an apical tooth not or scarcely curved and an absence of trigones (e.g., in *Schuster 36608, 36621, 36532*). This is the reverse of what is found here [i.e., in the British Isles]. In British materials there is rarely any difficulty in distinguishing between *patens* and *lamacerina*. *L. patens* is not very variable, being characterized by postical lobe "shape 1" [cf. Greig-Smith, 1954], curved lobular tooth and, almost always (in spite of their absence in the specimen from the type locality . . .), presence of trigones. *L. lamacerina*, in contrast, here shows a great deal of variability, mostly uncorrelated . . ."

Forest in the Southern Appalachians (*Schuster 23882*), "which shows not only features suggesting both *L. patens* and *lamacerina*, but some of the features of neotropical *L. glaucescens*. The lobules are larger [and narrower] than in the last species, but smaller than normal for *L. patens*. The apical tooth of the lobules agrees with that of *L. lamacerina* and *glaucescens*; the incised bracteoles with a sharp, often closed sinus agree with *L. glaucescens* and *patens*. The larger lobule size, as well as the large lobules of the female bracts quite eliminates *L. glaucescens*," leaving only *L. lamacerina* and "patens" under consideration. "On the basis of the lobule apex, and small lobule size, I should be tempted to put the plant in *L. lamacerina*—yet the European specimens of the latter . . . do not agree with it at all. . . . The gynoecia are [uniformly] terminal on long leafy branches, bearing 1 or 2 innovations, which may again be fertile, and never occur on short lateral branches. In this the plants are quite different from *L. patens*, in which 'cladogynous' inflorescences are common."

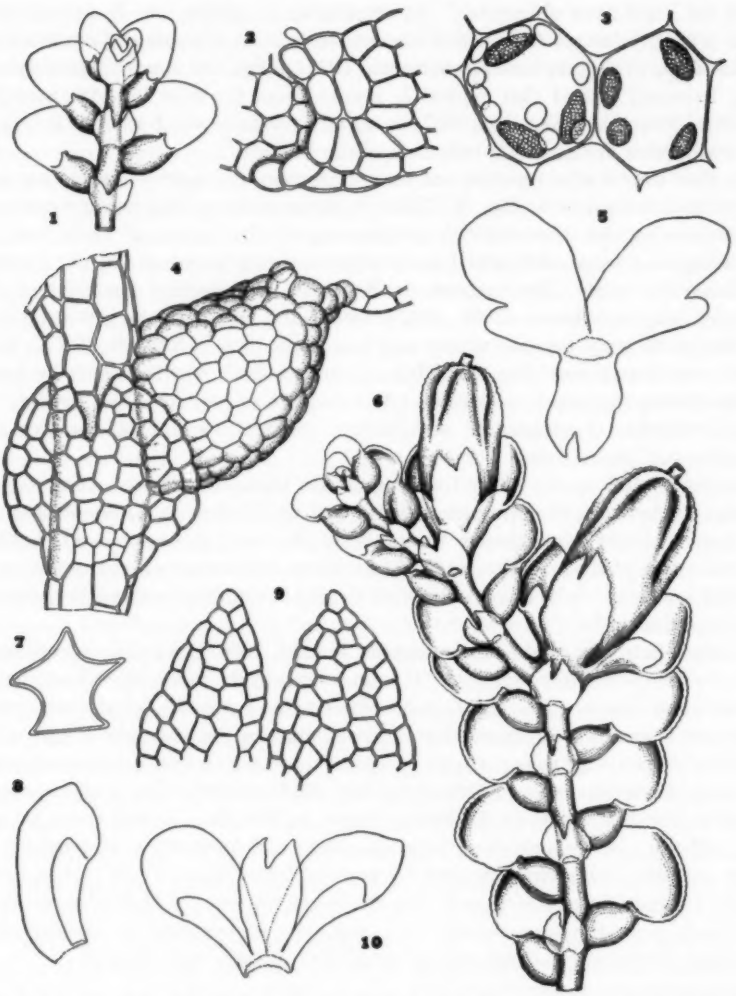

FIG. XXX. *Lejeunea lamacerina* subsp. *gemminata* Schust., extreme with perianths with distinct keels, grading towards subsp. *lamacerina*. 1. Apex of slender shoot (×58); 2. Lobule apex of same (×230); 3. Median cells with oil-bodies and, at left, chloroplasts (× *ca.* 825); 4. Lobule and adjacent underleaf, *in situ* (×195); 5, 8, 10. Bracts and bracteoles (×45); 6. Shoot with acrogynous perianth and solitary, fertile innovation (×45); 7. Cross-section of perianth, one-third from apex (×55); 9. Apex of bracteole (×200). (Figs. 1–3, from *Schuster 19901*, Balsam Gap, N. C., from same population shown in Fig. XXXI: 7–13; Figs. 4–10, from *Schuster 25014a*, Whitewater Gorge, N. C.)

Greig-Smith also corroborated that some of the Appalachian material "shows features . . . never seen in British material—the very inflated and almost keelless perianth shown in [*Schuster*] *36621* and *36608* and the gemminate innovations, in e.g., *36621*. *Schuster 28882* has a postical lobe shape of an unusual shape, narrower than anything I have ever seen." Greig-Smith concludes that "viewed against a background of the British material with which I am familiar I should regard all the material (of a series sent), except *Schuster 28882* as *lamacerina* rather than *patens*, but even so not really fitting in with *lamacerina* as I know it . . . *No. 28882* is perhaps nearer *patens* than *lamacerina* but I should hesitate very much to place it under that species. It is at least clear that we are dealing with a very troublesome group and one wonders whether it is amenable to orthodox nomenclatorial treatment!"

The wholly divergent nature of the Appalachian plants is also well brought out in correspondence the writer has had about this population with Dr. E. W. Jones, who compared a Virginian collection (*Schuster 38087*) with *L. lamacerina* (*L. planiuscula*). He noted the following differences: "the male inflorescences are far larger and more conspicuous than on any (British plants) . . .; the perianth . . . is stouter and is very weakly winged, whereas British plants have a rather slender perianth and long, strongly winged keels, and the lobule is larger . . . . British plants often have . . . the perianth on a short side branch with a weak innovation on the outer side; I did see one with two equal innovations as in your var. *gemminata*, but this appears to be exceptional. *Lamacerina* is also normally paler in colour with less chlorophyllose cells than (Appalachian material). . . . Thus my immediate reaction would be to doubt whether it was really the same as our *lamacerina*."

From the preceding, detailed account, it is therefore clear that the Appalachian plants are typically distinct from both *L. serpyllifolia* and typical *L. lamacerina*, in having: (a) perianths which are often weakly keeled and more inflated in appearance; (b) two subfloral innovations below many or most gynoecia that are found on leading branches; (c) the lobule with apical tooth usually short and straight as in *L. lamacerina*, but the lobule often rather large and strongly inflated, with involute apex and with a strongly arched keel and posterior notch, as in *L. "patens"*; (d) trigones normally small or absent, as in *L. lamacerina*, but unlike most *L. "patens"*; (e) often larger and more conspicuous androecia, which are sometimes intercalary on long, leafy branches.

VARIATION.—*L. lamacerina gemminata* is a highly variable plant. The variation is, in some cases, evidently environmental in origin, as, for example, in the size and shape of the lobule as related to lobe size. In other cases, such as the perianth form and development of keels, the variability may be uncorrelated genetic variation. The more salient extremes in variation may be outlined as follows:

Lobule size.—The size of the lobule varies to a large extent, as related to the size of the lobe. In shade forms of damp mountain summits, in the Southern Appalachians, the lobules may be very small. For example, in *RMS 19074a* (Balsam Gap, N. C., 6000 ft.) the lobule-size ratio may be only 1:7–10; in *RMS 37968* (Roan Mt., N. C., 6100 ft.) the ratio may be as low as 1:10–12 or less

(Fig. XXVIII: 4, 8–9; XXXI: 7). Associated with this tendency there are two others: the lobes "tend" to be unusually strongly dilated above the antical base, thus strongly and broadly, asymmetrically ovate, and therefore rather strongly narrowed towards the apex; and the underleaves tend to have a lunate sinus. Associated with this is also a fourth tendency, related to the reduced size of the lobule: the keel of the lobule is weakly convex, and the notch at its apex is very slightly developed. Normally, plants with "small" lobules show less convex lobes and less inflated-appearing lobules. In such cases, the free margin of the lobule appears much less strongly involute, and we have the lobule condition considered "typical" of *L. lamacerina* (Fig. XXVIII: 4, 8).

Contrastingly, plants from somewhat more exposed sites may have more inflated-appearing lobules of larger size, whose free margins appear more involute (Fig. XXX: 4, 6; XXXI: 2–5), as in *RMS 25014a* (Whitewater Gorge, N.C.), *RMS 28882 and 29461* (Linville Gorge, N. C.), and *RMS 31083c* (Grandfather Mt., N. C.). The lobule-lobe area ratio here is 1:5–8. Such plants may or may not show a lunate underleaf-sinus. The lobules, in all such cases, have more convex keels, and there is frequently a subrectangulate or even acute notch at the juncture of keel and free dorsal lobe (Fig. XXXIII: 6, 12).

The most extreme development of the lobule occurs in *L. serpyllifolia*-like extremes such as *RMS 36621* (Andrews Bald, N.C.) and *RMS 18301* (West Virginia). Here the lobules may be quite large and very much inflated (Fig. XXIX: 5–7, 11; XXXII: 11–12), up to half the length of the lobes, with the lobule-lobe area ratio 1:4–7 and the underleaves at times slightly smaller than the lobules! Associated with this, we find that the leaves, when not artificially flattened, have very convex lobes, and such strongly inflated lobules that their apical tooth is not visible without dissection (Fig. XXIX: 7, 12). Only when leaves are artificially somewhat flattened is the short and blunt apical tooth distinct (Fig. XXIX: 13; XXXII: 13). Such flattened leaves also demonstrate that the actual free lobular margin is at least narrowly appressed to the convex lobe, rather than being really involute to the apical tooth.

Strongly convex leaves, with large, strongly inflated lobules approaching those of *L. serpyllifolia*, can cause considerable confusion. Fortunately such extremes usually show the relatively short, nearly or quite straight, blunt apical tooth of *L. lamacerina* (Fig. XXIX: 13), i.e., we find a correlation between a *lamacerina*-type apical tooth and a *serpyllifolia*-like lobule shape. However, in *RMS 29461* (Linville Gorge, N. C.) a *serpyllifolia*-like lobule is correlated frequently with a curved apical tooth, as in *L. serpyllifolia*!

Apical tooth of lobule.—The large majority of plants of *L. lamacerina gemminata* agree with European and Oceanic *L. lamacerina* in possessing an apical tooth that is not or hardly curved, blunt, and relatively abbreviated (Fig. XXVIII: 11–12; XXIX: 13; XXXII: 13). As noted earlier, the form of the lobular apex is regarded by both Buch (1934) and Greig-Smith (1954) as of primary importance in separating these two species. However, plants from Balsam Gap, Blue Ridge, N. C. (*RMS 19074a*) otherwise very similar to *L. lamacerina*, particularly in the small lobules and the ovate, hardly falcate lobes

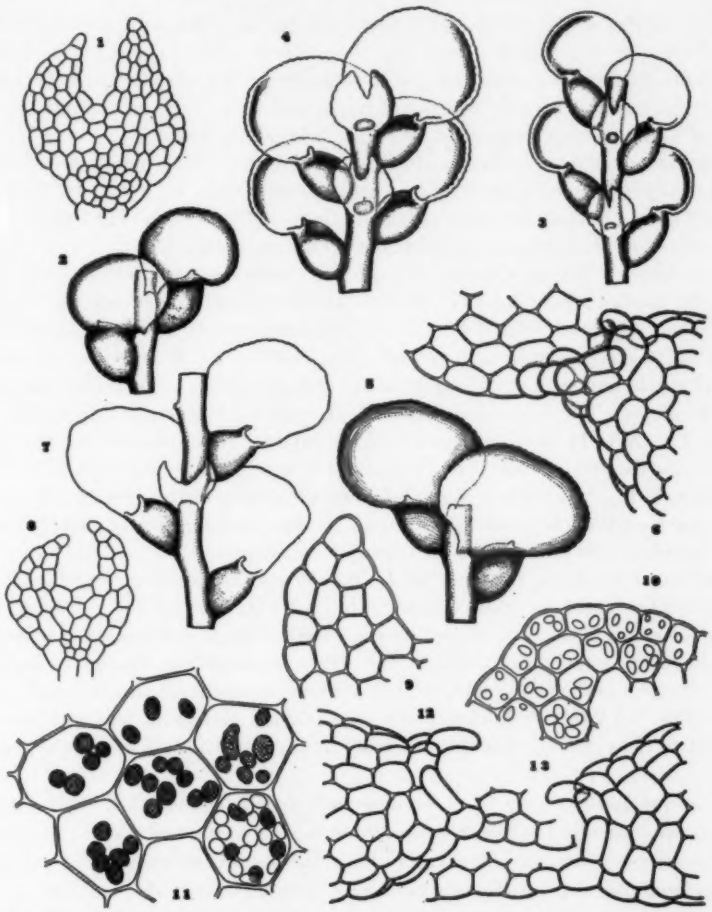

FIG. XXXI. *Lejeunea lamacerina* subsp. *gemminata* Schust., showing gradation towards *L. serpyllifolia* in lobule form. 1. Underleaf (×120); 2. Two leaves, *in situ*, from slender branch (×49); 3. Sector of large innovation, postical view (×49); 4. Sector of leading shoot, postical aspect (×49); 5. Same, antical aspect (×49); 6. Apex of lobule, not flattened (×232); 7. Small shoot, extreme with elongate apical lobular teeth (×62); 8. Small underleaf (×135); 9. Lobe of underleaf (×305); 10. Apex of lobe, with oil-bodies outlined (×275); 11. Median cells (×525); 12–13. Apices of lobules, with longest apical teeth found (×280). (Figs. 1–6 from *Schuster 38054a*, White Top Mt., Virginia; 7–13, from *Schuster 19101* and *19074a*, Balsam Gap, N. C.)

(Fig. XXXI: 7), may possess frequent lobules with a typical, *L. serpyllifolia*-like lobular apex, equipped with a curved, strongly elongated apical tooth, ranging up to 12–13 × 24–25μ in size (Fig. XXXI: 12–13).

Such curved and elongate apical teeth may occur on the same plant with more

normal, shorter and straight apical teeth, as, for example, in *RMS 29461* (Linville Gorge, N. C.). These plants also show the strongly inflated, large lobules, often with involute lobular apices, of *L. serpyllifolia*, yet they possess the weakly carinate perianths, broadly ovate leaf-lobes, and frequently gemminate innovations of *L. lamacerina gemminata*, to which they surely belong.

From this it can only be concluded that the American plants fail to show consistently the evidently nearly constant correlation of a "*serpyllifolia*-like lobule" with a curved, involute apical tooth vs. a "*lamacerina*-like lobule" with a short, blunt, straight, apical tooth that is not involute!

Underleaves.—The underleaves in typical *L. lamacerina* are very often broadly, lunately bilobed (Fig. XXVII: 10–12). In the subsp. *gemminata* the sinus is more often U-shaped (Fig. XXIX: 7, 11–12), or narrowly V-shaped (Fig. XXX: 4, 6), but occasionally broadly lunate (Fig. XXXI: 7). It is doubtful that the variation has any systematic significance, and it appears to be uncorrelated.

Lobe shape.—The lobe in *L. lamacerina*, typical, is broadly asymmetrically ovate (Fig. XXVII: 8–9), with a relatively broadly rounded apex. In the subsp. *gemminata* the ovate form is more marked in many cases (Fig. XXVII: 15–16; XXVIII: 8–11), but there is a good deal of variability in this respect. It is probably true that the lobes tend to be, on an average, more narrowly rounded at the apex in subsp. *gemminata* than in typical *L. lamacerina*.

Bracts and bracteoles.—In typical *L. lamacerina* the bracts often bear broadly obovate lobes and very small lobules (Fig. XXVII: 5–7, 13–14), although there is some variation in this respect (see p. 168). Subsp. *gemminata* is relatively uniform in all collections studied: the lobes are lingulate-oblong to lingulate-obovate, with rather large lobules that average more than half the length of the lobes (Fig. XXVIII: 7; XXIX: 8–9). Not enough European material has been studied to demonstrate whether a wholly uniform distinction is possible on this basis.

Gynoecial position.—As has been demonstrated, *L. lamacerina*, typical, rarely or only sporadically has acrogynous gynoecia with two innovations. The American subspecies *gemminata* is very variable in the number of innovations produced, but gemminate innovations can always be demonstrated. The number of such innovations ranges from less than ten per cent to as high as 60–70 per cent of all acrogynous inflorescences. In some American plants, cladogynous innovations appear to be absent (e.g. *RMS 36608*, Andrews Bald, N. C.; *RMS 28882*, Linville Gorge, N.C.); in others they occur rather frequently or rather infrequently (e.g. *RMS 37968*, Roan Mt., N. C.; *RMS 29461*, Linville Gorge, N.C. [Fig. XXVIII: 3; XXXIII: 9]). In the latter case, however, the cladogynous inflorescences are often on *elongate* lateral branches bearing 3–4 pairs or more of more or less normal leaves before producing bracts, only occasionally on abbreviated lateral branches!

Associated with the latter condition, i.e. the occurrence of gynoecia on leafy lateral shoots, we occasionally find elongate, spicate androecia terminal on the leading axis, from which the gynoecial branches arise (Fig. XXVIII: 3). This is clearly shown in the Roan Mt. material (*RMS 37968*). Inversely, when the

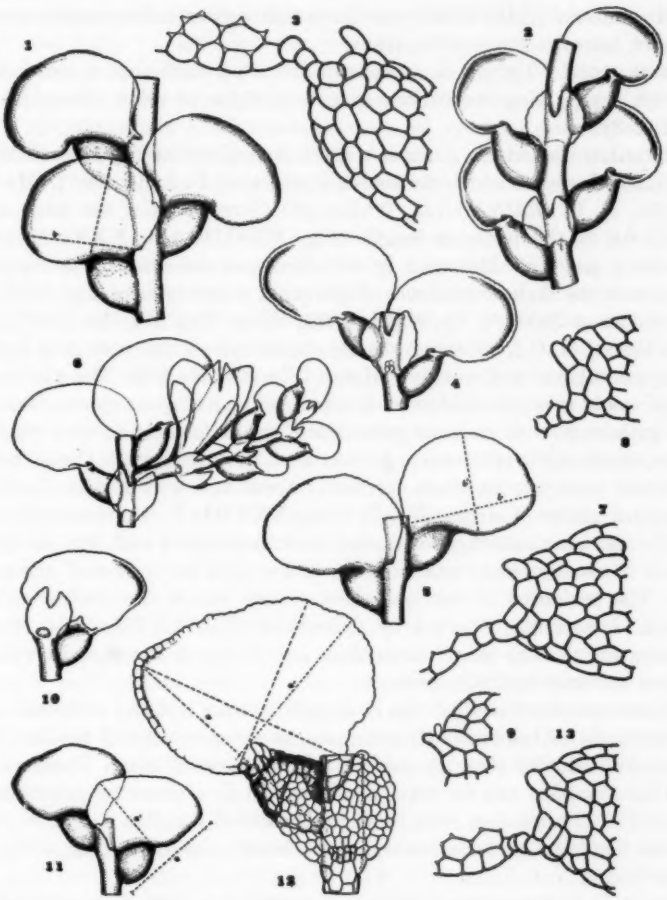

FIG. XXXII. *Lejeunea serpyllifolia* (Dicks.) Libert. 1. Shoot-sector, antical view (×55); 2. Same, postical aspect of smaller shoot (×55); 3. Apex of lobule, not flattened (×170); 4. Shoot-sector of large plant, postical view (×40); 5. Same, antical view (×40); 6. Shoot-sector with cladogynous branch (×33); 7. Apex of lobule, weakly flattened (×170); 8–9. Apices of lobuli, strongly flattened (×170). *Lejeunea lamacerina* subsp. *gemminata* Schust. 10. Leaf and underleaf, *in situ* (×33); 11. Shoot-sector, antical aspect (×33); 12. Leaf and underleaf, *in situ* (×72); 13. Apex of lobule, moderately flattened (×170). (Figs. 1–9, *L. serpyllifolia*; 1–2, from Schiffner, Hep. Eur. Exsic. 1067, Killarney, Ireland; 3–9, from coll. of E. W. Jones, Kerry, Ireland. Fig. 10–13, *L. lamacerina gemminata*, from *Schuster 18301*, West Virginia.)

gynoecia are found only on leading, leafy branches, the androecia often form small, sessile lateral branches and bear only 2–4 pairs of bracts (Fig. XXIX: 6). Whether or not these two contrasting conditions are of systematic importance is very questionable; at any rate they are not always correlated. For example, the

Roan Mt. material (*RMS 37968*) may have cladogynous inflorescences associated with short, lateral androecial branches!

Perianth shape.—Typical *L. lamacerina* has a perianth that is slenderly obovoid, with sharp, wing-like carinae extending down to below the middle (Fig. XXVII: 2–3).

In the subsp. *gemminata* there is a great deal of variability in both shape of perianth and degree to which the keels are produced. In some cases (*RMS 37968*, Roan Mt., N. C.; *RMS 25014a*, Whitewater Gorge, N. C.) the keels descend fully 0.5–0.6 of the perianth length (Fig. XXVIII: 4–6; XXX: 6), and are rather sharp and high. However, in well-developed material, particularly of the extreme with the highest incidence of gemminate innovations (e.g. *RMS 36621*, *36608*, Andrews Bald, N. C.; *RMS 38087*, White Top Mt., Va.; *RMS 29461*, Linville Gorge, N. C.), the perianths are almost cylindrical, with only the apices obtusely pentagonal and weakly carinate (Fig. XXIX: 1–6). The plants of this last type would give the impression of representing a distinct species, were it not for the gatherings with carinate perianths of the *L. lamacerina* type which have been frequently made in the same general area. In most cases, it should be noted, the perianth beak is quite short, formed of about two tiers of cells. However, in the atypical plants of *Austin No. 97* (Fig. XXXIII: 1), the unusually slender perianths also bear a strongly elongated beak. Associated with this, the perianth keels are unusually sharp and distinct, and extend for over half the perianth length! The perianths of this collection closely match the Scottish plants of typical *L. lamacerina* collected by Crundwell (Fig. XXVII: 2–3), effectively demonstrating that no sharp distinctions can be drawn between European and American material in this respect.

Leaf and underleaf-margins.—In *L. serpyllifolia* the leaf and underleaf-margins are consistently rather obviously crenulate, as a consequence of the fact that the cells are individually strongly convex, often almost globose. There are times when this condition can be totally matched in *L. lamacerina gemminata* (e.g. *RMS 31083c*, Grandfather Mt., N. C.; *RMS 28882*, Linville Gorge, N. C.), but often the leaf- and underleaf-margins are hardly crenulate (e.g. *RMS 29461*, Linville Gorge, N. C.).

Leaf cells.—*L. lamacerina*, typical, normally is a leptodermous and rather hyaline plant. This is also the case, normally, in the subsp. *gemminata*, as in *RMS 29461* (Linville Gorge, N. C.) where trigones are minute. However, in the plants of Austin's *Hep. Bor.-Amer. No. 97* (locality?) and in *RMS 31083c* (Grandfather Mt., N. C.) there are very large trigones and coarse intermediate thickenings present, exactly as is typical of *L. serpyllifolia* (Fig. XXXIII: 7, 13)! Such plants further approach *L. serpyllifolia* in the large lobules with strongly involute free margins, and in the sharply notched posterior leaf margins! Indeed, except for cell size, these plants can hardly be separated from *L. serpyllifolia*!

Cell Size.—The American material, finally, was all assigned to *L. lamacerina* on the basis of the more pellucid cells, closely resembling those of *L. lamacerina*, but perceptibly larger and less opaque than in *L. serpyllifolia*. In the American material the marginal cells average (18) 19–21.5μ, tangentially measured. This is

almost identical with the few European specimens of typical *L. lamacerina* studied (see Table I), although the Scottish plants collected by Crundwell, which are clearly *L. lamacerina* in other respects, have considerably smaller cells and thus approach *L. serpyllifolia*. It must be emphasized that after several weeks of detailed study of all available material, no final conclusion had been arrived at regarding the disposition of the American plants, although it was felt that they fell closer to *L. lamacerina*. This problem was finally resolved by their uniformity in cell size.

The European *L. lamacerina* in general showed equally large and pellucid cells, only the Scottish material collected by Crundwell showing smaller cells. These plants, however, clearly showed the characters of *L. lamacerina*, and, indeed, closely approached the nearctic race, subsp. *gemminata*, in some ways such as the high incidence of acrogynous inflorescences, a considerable number of which bore two innovations, and the rather large androecia. If it were not for certain features, these plants might easily pass for subsp. *gemminata*. However, they had bracts with short, reduced lobules, leaves with broadly rounded apices, smaller lobules than typical for *L. lamacerina gemminata*, and strongly quinque-carinate, somewhat winged perianths, with the carinae descending for 0.65–0.75 of the perianth length. These plants, although clearly *L. lamacerina*, show that the characters at first considered most typical of the subsp. *gemminata* may also be found in European material, although not all the features of the American plants are to be found in any single collection of the European species.

The above discussion has served to show, it is hoped, that much of the variability of *L. lamacerina* is quite uncorrelated, and that little or no systematic significance can be attributed to it. Greig-Smith (1954) showed this to be true for the much less broadly varying European populations which he studied. It is also hoped that the identity of the exceptionally variable American plants as *L. lamacerina* s. lat. is firmly established. The close similarity of much of the American material to *L. serpyllifolia* should not obscure the fact that in the crucial features of cell size this material can only be placed in *L. lamacerina*. Only one important question remains to be answered: should the American plants, with their deviant features (and their often great similarity in facies to *L. serpyllifolia*, with the crucial characters as in *L. lamacerina*), be regarded as wholly distinct from *L. lamacerina* or not? Study of the large series of American plants has firmly convinced the writer that no sharp and uniform distinctions exist between European and American populations of *L. lamacerina*; the variability of the two populations is admittedly in differing directions, but they remain separable, in critical cases, only on the basis of an evaluation of the constellation of characters by which they differ. In isolated cases, the keys here given will surely prove inadequate for this purpose.

Lejeunea serpyllifolia (Dicks.) Libert

Jungermannia serpyllifolia Dicks., Fasc. Pl. Crypt. Brit. **4**: 19, 1801 (as to type!; not *Lejeunea serpyllifolia* Libert, 1820!).
Pandulphinius serpyllifolius S. F. Gray, Nat. Arr. Brit. Plants, **1**: 689, 1821.

Lejeunea patens Lindb., Acta Soc. Sci. Fenn. **10**: 482, 1875; Moore, Proc. Roy. Irish Acad. II, **2**: pl. 43, 1877; Pearson, Hep. Brit. Isles, I: 47, II: pl. 11, 1899, 1902; Macvicar, Stud. Hdb. Brit. Hep. Ed. II: 432, *cum* fig., 1926; Buch, Rev. Bryol. (n.s.) **7**: 246, fig. 8, 10, 15, 1934.

Plants in thin, *pale to whitish-green* patches, *strongly glistening* when dry, occasionally creeping among other bryophytes. Plants decumbent to prostrate, 7–12 mm. long × *525–725 (800–950)μ wide*, irregularly and sometimes freely branched; rhizoids relatively scarce; stem 70–85μ in diam.; ventral cortical cells 24–35μ wide. Leaves loosely to distinctly imbricate, *erect-spreading at base* but then abruptly quite widely spreading, the *lobes strongly falcate and convex, except for the depressed, nearly plane portion lying over the large lobules.* Dorsal lobes *relatively slender, falcate, strongly ovate-oblong, widest near the apex of keel, or near middle of lobe*, above the antical base hardly dilated, *much less so than in* L. lamacerina, *the antical margin nearly evenly arched* from base to the broadly rounded apex, *which is usually markedly decurved, extending across but rarely beyond the stem*, the antical face of the stem consequently nearly or quite hidden beneath the shingled leaf-bases; postical margin also evenly curved into the apex, *at its base at a more or less sharp angle with the strongly convex keel* (on well-developed shoots the angle less than 90°, the *posterior leaf-margin consequently appearing sharply and often deeply incised*, the angle often 100–120° on less robust shoots); length of lobe, from keel, up to (350) 400–435 (500)μ, width (240) 260–340 (350–370)μ (maximal width, measured at level of postical notch), the length *ca.* 1.2–1.3× the width; *margins of lobe distinctly crenulate*, owing to projecting cells. *Lobule constantly large, strongly inflated throughout*, ovate, from 170μ long × 100–115μ wide up to 200–215μ long × 140–160μ wide, its *length 0.4–0.55 times the length of dorsal lobe* (on branches often 0.55–0.65); *free margin involute to the apical cell* (which is not visible, when leaves are *in situ*), the apex lunulately truncate; apical cell *usually elongate, curved, ca.* 15 × 24–28μ; situated in a small notch at its proximal base, the hyaline papilla; *keel very strongly arched*, more or less crenulate owing to bulging cells; *sinus of lobule apex continuous with postical lobe margin.* Marginal cells usually *averaging (13) 14–16* (19.2)μ, in the lobe-middle 21–25 × 24–30μ, a group of cells at the base strongly elongated and 16–20 × 40–45μ; cells varying from nearly leptodermous with small, concave-sided trigones and no intermediate thickenings, to (more *usually*) *mesodermous*, with nodular, somewhat bulging trigones and *frequent intermediate thickenings; oil-bodies 3–6 per cell*, occasionally up to 8, varying from ovoid to elliptical, occasionally spherical, formed *of distinct, more or less protuberant spherules. Underleaves relatively small, clearly distant* (on mature shoots the intervals between subequal to the underleaf-length), rotund or subrotund, narrowed to base, from 150–160μ wide × 130μ long to 160–180μ wide × 150–160μ long, to a maximum of 190–195μ wide × 160–220μ long, *their area averaging 0.7–1.0 times the area of lobule* (length 0.65–1.0× the length of lobule); the rather *rounded sinus* descending to middle, the lobes erect *or weakly connivent*, triangular, terminated by a single cell or *often blunt, 4* (rarely 5) *cells wide at base, the margins distinctly crenulate* owing to bulging cells; sinus descending to within (3) 4–5 cells of the small rhizoid-initial field.

Autoecious. Androecia usually on short, leafless, lateral branches, *inconspicuous, small*, the bracts in 2–4 imbricated pairs; bracts shallowly, subequally bilobed, each with a long, inflated, convex keel; diandrous. Female inflorescences *relatively infrequent on an elongate, leafy branch* (bearing 1, very rarely 2, subfloral innovations; the innovations often soon again floriferous), *more frequently on a short, lateral branch*, which always bears a single innovation. Bracts loosely complicate, quite unequally bilobed, the lobe erect-spreading, lingulate to narrowly obovate-oblong, rounded or broadly obtuse at apex, the margins more or less distinctly crenulate (as on leaves); lobule *ca.* 0.6–0.75× the length of the lobes, narrowly lingulate, rounded or obtuse or subacute at apex, *free for less than ⅓ of its length*; bracteole free or virtually so, oblong to obovate, ¼–⅓ bilobed, the lobes and sinus acute, the margins crenulate. Perianth exserted for 0.5–0.6 of its length, *narrowly obovoid-obclavate*, 350–370μ wide × 750–800μ long (rarely up to 450–500μ wide × 900μ long), *sharply 5-carinate in the distal 0.4–0.6, the keels often narrowly winged*, gradually narrowed in their terete basal third, the distal two-thirds subequal in width (including the keels), or only very

slightly wider beyond the middle; keels margined by 2 rows of protuberant cells, distinctly crenulate, *often with some of the cells conically elevated* (the keels then denticulate); beak elongate, the terminal cells slender, *ca.* 6–8μ wide × 27–31μ long; subterminal cells internally produced.

TYPE: British Isles; the type of *L. patens* from Ireland (Lindberg).

The history of this species is involved. Lindberg (1875) described it as a new species, *Lejeunea patens*, because he (and previous workers, such as Libert) had presumed that *Jungermannia serpyllifolia* was identical with the plant now known as *L. cavifolia*. However, four years later (Musci Scand., p. 2, 1879) Lindberg found that the type of *J. serpyllifolia* was identical with his *Lejeunea patens*. He did not place *L. patens* in synonymy under *serpyllifolia* because Libert (1820) had used the combination *L. serpyllifolia* (Dicks.) Libert for the plant now known as *L. cavifolia*. Furthermore, she had been followed in this usage almost consistently in the fifty succeeding years. This has led to reasoning, such as Evans' (1902, p. 150), that the "name '*Lejeunea serpyllifolia*', however, cannot now be taken up for *L. patens*, on account of the older *L. serpyllifolia* of Libert." Unfortunately, the existing rules of nomenclature place sufficient emphasis on the rules of priority that we do have to take up, for *L. patens*, the older specific name of *L. serpyllifolia*. The fact that Libert and, after her, other workers, were either careless or in error as regards *the application* of Dickson's name *J. serpyllifolia* is not germane to the matter. It has been clear, since 1879, exactly what Dickson meant by his *J. serpyllifolia*, and his name cannot be considered as dubious in any way.

The confused nomenclature of this species has not been rendered clearer by Frye and Clark (1947, p. 798), who list, as synonyms, *Lejeunea serpyllifolia* var. *americana* Lindberg, *L. flava* subsp. *albida* Spruce, "according to Evans," and *L. americana* Evans, "in most part." As Evans has shown (1911), all three of these names are clearly to be considered synonyms of *L. flava*.

DISTRIBUTION.—A species of oceanic affinity, occurring peripheral to the North Atlantic, from the southwest coast of Norway (lat. 62°; the northernmost limit of the species) southward through the Shetland Isls., the Faroes, Scotland and England, Ireland, to Spain and Portugal (Casares-Gil, 1919, p. 711; Buch, 1934, p. 246), and recurring in the Azores (Allorge, 1948).

The North American distribution of this species is wholly unknown; according to my interpretation of it, it is absent in America, although it was reported from our area as early as 1902 by Evans and has been reported many times since. The reason for this lies in the consistent confusion of this species with *L. lamacerina*. It is not probable that this confusion will soon be wholly dispelled, since, as is emphasized elsewhere, the American phase of *L. lamacerina* appears to grade into *L. serpyllifolia*. The first possibly valid report of "*L. patens*" from North America appears to be that of Buch (1934, p. 246), of Austin's *Hep. Bor.-Amer. No. 97* (issued as *Lejeunea cavifolia*).[26] This material, unfortunately, bears no accurate label, and, judging from the admixture found, came partly from the

[26] The number of this exsiccatae in the Helsingfors herbarium is, according to Buch, *L. patens*. In the University of Michigan herbarium this number contains two small patches, one with a plant approaching *L. serpyllifolia* (= *patens*); the other, from bark, represents *L. flava* admixed with *Frullania obcordata*!

coastal plain (*L. flava*), and partly from the mountains (doubtful *L. serpyllifolia*). From my experience with the group, plants closely approaching true *L. serpyllifolia* are rare, and very sporadically found in the mountains, and in almost all cases show at least an "approach" to *L. lamacerina*. Among such plants are the following:

NORTH CAROLINA: BURKE CO. (Linville Gorge, *ca.* 2500 ft., below the High Falls, *RMS 29461*); Caldwell Co. (Grandfather Mt., near summit, at 5800 ft., *RMS 30183c*).

The above plants (Fig. XXXIII) are all critical, and will need reinvestigation when much longer series become available. In the material of *RMS 29461* the lobules are often large and strongly inflated, up to 0.45–0.5 times the length of the lobes; the lobular apices are involute, with a curved, involute apical tooth (thus of the "*serpyllifolia*-type"); the gynoecia are rather frequently on short lateral branches (Fig. XXXIII: 9); and the leaf-cells are here and there distinctly collenchymatous, although rarely with intermediate thickenings (Fig. XXXIII: 11). All these are "*serpyllifolia*" features. However, the dorsal lobes are more or less broadly ovate, of the *lamacerina* shape; gynoecia are most frequent on long, leafy branches or leading stems, and may occasionally show two innovations; and on main stems the lobes may be up to 8–10 times the area of the lobules (Fig. XXXIII: 10). These are clearly "*lamacerina*" features, and I am disposed to regard the plants as an extreme of *L. lamacerina* subsp. *gemminata*.

Equally dubious is the disposition of the plants of *RMS 30183c*. These show the very large inflated lobules, with incurved elongate apical cells, of *L. serpyllifolia*; they also show unusually convex leaf and underleaf cells, with consequently strongly crenulate leaf and underleaf margins (Fig. XXXIII: 12); they are also characterized by the collenchymatous cells with frequent intermediate thickenings (Fig. XXXIII: 13). On these bases, the plants could easily pass for *L. serpyllifolia*, and they have nearly the facies of this species. Yet, the leaf-lobes have the characteristic broadly ovate shape of *L. lamacerina*, and the gynoecia appear to be always on elongate leafy branches or leading shoots, with occasionally two innovations developed!

These plants, as well as Austin's *No. 97* (Fig. XXXIII: 1–8), which Buch would consider to be *L. patens*, have uniformly more pellucid cells, larger in size, than in European *L. serpyllifolia* (= *L. patens*). Austin's *No. 97* has them ranging from 20.8μ to 23.0μ on the margins, on an average; in *RMS 29461* they average 20.8–23.5μ and in *RMS 30183c*, 19.6–23.0μ. In typical "*L. patens*" the marginal cells average 13.9–19.2μ. On this basis, therefore, all the American material, including the dubious and seemingly intermediate types cited above, clearly falls into *L. lamacerina* rather than "*L. patens*."

The species has been reported, as *L. patens*, from Newfoundland (Evans, 1902), Nova Scotia (Macoun, 1902; Brown, 1936), Maine (Lorenz), Connecticut (Lorenz, 1926, 1927; Evans, 1923); Ohio (Conklin, 1926); Virginia (Patterson, 1949); West Virginia (Ammons, 1940); Kentucky (Fulford, 1936), North Carolina (Blomquist, 1936), Tennessee (Sharp, 1939; Clebsch, 1954), and northern Georgia (Parker, 1941). These reports are possibly all to be referred to *L. lama-*

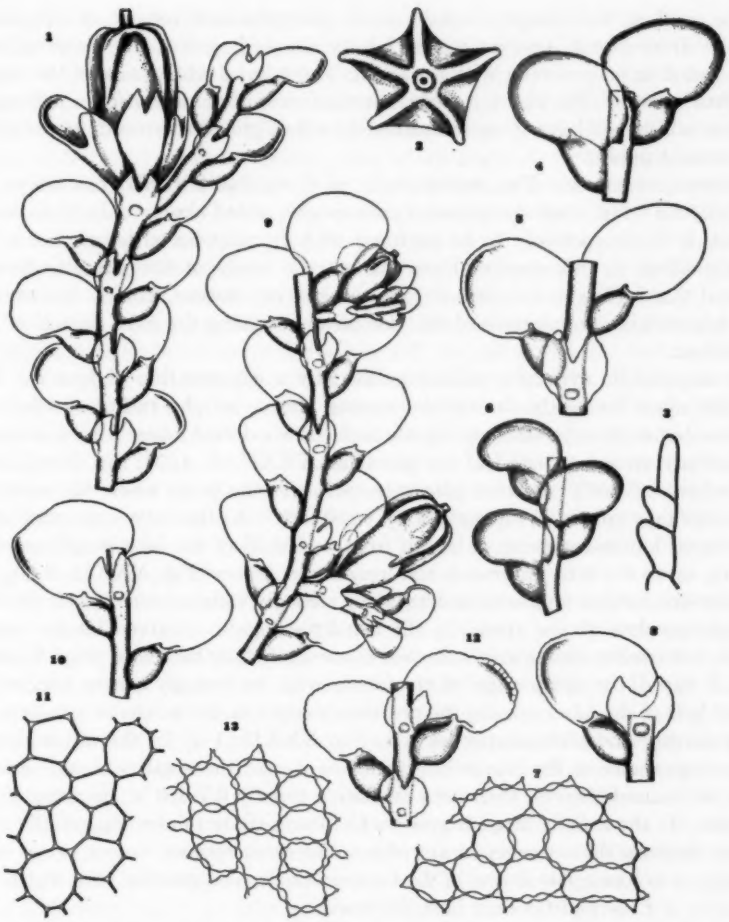

FIG. XXXIII. *Lejeunea lamacerina* subsp. *gemminata* Schust., with marked superficial intergradation to *L. serpyllifolia*. 1. Shoot, with acrogynous perianth and single innovation (×39); 2. Apex of perianth (×57); 3. Section of beak (× *ca.* 280); 4. Mature shoot-sector, antical aspect (×46); 5. Same, postical aspect (×46); 6. Sector of weak secondary axis, antical aspect (×46); 7. Median cells (×263); 8. Leaf and underleaf, *in situ* (×46); 9. Shoot with two cladogynous perianths (×27.5); 10. Large shoot, sector in postical aspect (×31); 11. Median cells (×263); 12. Large shoot, sector in postical aspect (×41); 13. Median cells, showing maximal development of collenchyma (×263). (Figs. 1–8, from Austin, Hep. Bor. Amer. 97, = *L. serpyllifolia* according to Buch, 1934; 9–11, from *Schuster 29461*, Linville Gorge, N. C.; 12–13, from *Schuster 31083*, Grandfather Mt., N. C.)

cerina, and at least largely belong to it. All published reports of "*Lejeunea patens*" from North America which I have checked against the material have been found to be incorrect, with the single, somewhat doubtful case of the report of Buch (1934).[27] The above reports, therefore, are of value chiefly in indicating reports which will have to be re-examined in the light of the results obtained in the present paper.

DIFFERENTIATION.—The recent study of Greig-Smith (1954) has shown *L. serpyllifolia* to be a relatively stenotypic species, allied closely only to *L. lamacerina*. It is also possibly to be confused with *L. cavifolia*, although not at all closely allied to this species. Even though the study of Greig-Smith demonstrated that in England *L. serpyllifolia* was sharply distinct from *L. lamacerina*, the Appalachian populations of this complex are among the most critical of our *Lejeuneae*.

L. serpyllifolia typically is distinguished by a constellation of features that usually allow its ready distinction, among them: (a) the rather slender and narrow but extremely strongly falcate and convex dorsal lobes, with a strongly but evenly arched antical leaf margin (Fig. XXXII: 1, 4, 5); the dorsal lobes are suberect basally and then abruptly spread to the point where the apices of the lobes may spread at an angle of up to 90–130°; (b) the very large, uniformly developed lobules, varying in length from 0.45–0.55 of the lobe length on stem leaves, up to 0.5–0.65 on branch and innovation leaves (Fig. XXXII: 2, 4); the lobules are further characterized by their strongly inflated form, with the free margin involute to the apex; (c) the usually elongate, incurved lobular apical tooth, not readily visible unless the leaves are artificially flattened (Fig. XXXII: 2–4, 7–9); (d) the sharp angle of the lobule, with its strongly convex keel, to the distal half of the lobe, causing the posterior margin of the leaves to appear to be very sharply and often deeply incised (Fig. XXXII: 1–2, 5); the almost geniculate appearance of the leaves in extreme cases; (e) the small size and remoteness of the underleaves, their area averaging usually 0.7–1.0 × the area of the lobules; (f) the usually large trigones and intermediate thickenings of the cells. These features do not recur in any other American species, except, to a lesser extent, in xeromorphic forms of *L. lamacerina*, in conjunction with which the features of *L. serpyllifolia* are best discussed.

The dorsal lobe of *L. serpyllifolia* is more narrow and slender than in all mature phases of *L. lamacerina*, with the antical margin above the base evenly arched and not abruptly dilated; the dorsal lobe may be geniculate in form. The peculiar form is due to the fact that the depressed basal portion of the lobe, lying over the lobule, is erect-spreading (*ca.* 40–50°), while the free distal portion of the lobe is almost or quite at right angles to the stem (sometimes spreading at 95–110° or

[27] The species has also been reported from as far inland as Lake Timagami, Ontario (Cain and Fulford, 1948). Study of a duplicate (*Cain No. 3059*, det. M. F. Fulford) reveals the material to be *L. cavifolia*. The larger underleaves, up to 220μ wide, with the lobes 6–8 cells broad at base, and the persistent, minute oil-bodies, eliminate *L. patens* from consideration. Frye and Clark (1947, p. 800) report an "Examination" from the outer Piedmont of North Carolina (Durham, *leg.* H. L. Blomquist); this report represents an error, the *L. patens-lamacerina* complex being strictly montane as far south as North Carolina.

more with the stem, measured along the midline of the lobe). The lobule in this species is extremely large, especially on weaker or juvenile stems (where its length may considerably exceed half the lobe length).[28] It is constantly inflated, under apparently even the most humid conditions, and typically is nearly as large as (or sometimes barely larger than) the adjacent underleaves in area. The lobule is normally erect-spreading, lying at an angle of 40–50° with the stem. The portion of the dorsal lobe lying over the lobule is not convex, and may indeed appear depressed above the anterior margin of the lobule; by contrast, the distal portion of the lobe, lying distad of the lobule, is strongly and characteristically convex. Although the dorsal lobes may be convex in *L. cavifolia*, they never attain the convexity often exhibited by those of *L. serpyllifolia*.

The lobule of *L. serpyllifolia* is usually inflated throughout, with the free margin appearing involute up to (or beyond) the apical cell. On mature leaves, the keel is extremely strongly arched, and at a sharp angle with the free posterior margin of the dorsal lobe; in such cases the subtruncate apex of the lobule lies in an almost continuous line with the free posterior margin of the lobe (Fig. XXXII: 2, 4). This mode of orientation of the lobular apex was emphasized by Buch (1934) as one of the features separating *L. serpyllifolia* from the allied *L. lamacerina* (= *L. planiuscula*) (Fig. XXXII: 10). Unfortunately, the more xeromorphic extreme of *L. lamacerina*, in North America, may almost or quite agree with *L. serpyllifolia* in this feature.

The perianth of *L. serpyllifolia* usually shows obviously sharp, crenulate keels that extend down for over two-fifths of the perianth length; frequently they descend below the middle. The perianth is distinctly oblong to obovoid-clavate, and widest above the middle, or at least parallel-sided distally. Unlike that of *L. cavifolia*, it is never clearly widest near the middle.

The distinction of the species from *L. cavifolia* is accomplished most easily on the basis of the oil-bodies. These are segmented, few per cell, and usually disintegrate within a few months after the plant dies (when dry). In the oil-bodies, and in the relatively small underleaves, as well as in the perianth-form, *L. serpyllifolia* agrees more closely with *L. lamacerina* than with *L. cavifolia*. Buch (1934) and Greig-Smith (1954) have dealt in detail with the separation of *L. serpyllifolia* from *L. lamacerina* (= *L. planiuscula* of Buch).

In addition to the preceding distinctions (from *L. cavifolia*), involving (a) a larger lobule; (b) smaller underleaves; (c) a more convex free dorsal lobe, usually quite falcate in form or even geniculate; (d) an obpyriform-clavate perianth; (e) crenulate perianth-keels; (f) segmented, large and few oil-bodies per cell, a

[28] The lobules on innovations and weak stems may be extremely large, their surface area equalling half that of the lobe, i.e. in postical aspect the lobular outline will have an area equal to that of the portion of the lobe exposed beyond it! Even in the most extreme individuals of *L. lamacerina* such very large lobules, and correspondingly reduced lobes, are never produced. There is, furthermore, a subtle yet real distinction in lobule form which even the most carefully executed figures will hardly show; in many cases the lobular cells are elongated and oblong or oblong-hexagonal in the central portions of the lobules, while they are everywhere subisodiametric in *L. lamacerina*. These differences, although exhibiting a certain nicety, are real and easily evident to the practiced eye.

number of other differences, less reliable in nature, are usually evident. Among these are: (a) leaf-margins, and to a lesser extent underleaf-margins, strongly crenulate, the leaf-cells being more obviously convex; (b) slightly smaller leaf-cells, those of the margins especially averaging smaller; (c) constantly strongly shiny texture when dry; (d) paler, often more yellowish-green color. In spite of all these differences, the two species occasionally are distressingly similar, and Macvicar (1926, p. 433) went so far as to state, "I am doubtful if the two plants can always be separated." However, the cytological differences in all cases are quite constant.

VARIATION.—*L. serpyllifolia* is closely allied to *L. lamacerina*, forming with this a complex that shows a distressing range in variation in several features, among them (a) form and length of the perianth-keels; (b) form and position of the apical tooth of the lobule; (c) form of underleaves; (d) position of inflorescences; (e) number of subfloral innovations.

In typical European material of *L. serpyllifolia* (as typified by a plant collected by E. W. Jones at Glenbeigh (Kerry, Ireland, Sept. 1951) the sharp perianth-keels are typically narrowly winged, surmounted by two rows of cells, with a longitudinal delicate groove separating them. Each of the cells in these two rows is gibbous, or may actually be conically produced, with the consequence that the perianth-keels are finely denticulate. In the form of the keels, these plants closely approach *Crossotolejeunea bermudiana*. By contrast, American plants which have been considered conspecific, but which I regard as representing *L. lamacerina*, show merely convex cells along the perianth-keels, which are therefore merely crenulate. These plants vary widely in perianth shape and length of keels; in many cases the latter are quite low and short.

The European material of *L. serpyllifolia* is characterized by having the lobule involute up to, *and including*, the apical tooth. The apical tooth, furthermore, is formed of a cell that is elongate, and usually somewhat curved. Consequently, the lobule opens *via* a subcircular, small opening, with the apical tooth curved and appressed to the lobe. This quite characteristic feature is emphasized by both Buch (1934, see fig. 10) and Greig-Smith (1954, see fig. 2) as separating *L. "patens"* from such allied species as *L. lamacerina* and *L. cavifolia*. Such lobules, strongly inflated throughout, with the whole anterior margin and apical tooth involute, are characteristic of all the European plants I have studied. By contrast, a series of American plants (*RMS 25014a, 18301, 19901*) show a lobular apex that is usually disturbingly different. The American plants exhibit lobules which, even when with totally involute free margins, possess an inconspicuous apical tooth, which is not or only exceptionally strongly elongate and not curved outward. In this respect, the American plants often closely approach *L. lamacerina*, i.e., although they have a lobule-shape of the "*serpyllifolia*-type," the apical tooth is of the "*lamacerina*-type."

The underleaves of the European plants are very frequently provided with a somewhat lunate or rather broadly U-shaped sinus, although this is not invariably the case. Most American plants, however, show an acute sinus or narrowly U-shaped sinus; this again is subject to some variation and intergradation.

The position of the female inflorescences shows disturbing discrepancies between the nearctic and holarctic plants that have been held to be *L. "patens."* The typical material of *L. serpyllifolia* from Kerry, Ireland (E. W. Jones, 1951), for example, exhibits almost wholly cladogynous inflorescences, which are usually on very short lateral branches (Fig. XXXII: 6), rarely on leafy lateral branches. No acrogynous gynoecia could be found at all, and none were found with two subfloral innovations.[29] Associated with this, the unusually large and conspicuous androecia were found situated, in most cases, close to the gynoecia. The American material that has been erroneously referred to *L. "patens"* shows an overwhelming percentage, 70–100 per cent on various gatherings, of inflorescences situated on leading leafy shoots, some of which in almost every instance show two innovations.

The above observations, as well as others, have led to the conclusion that all the examined American material is more correctly assigned to *L. lamacerina*, under which it is treated in detail.

Lejeunea cavifolia (Ehrh.) Lindb. emend. Buch

Jungermannia cavifolia Ehrh., Beitr. **4**: 45, 1779.
Jungermannia clavaeflora Nees, *in* Martius, Fl. Crypt. Erlang., 137, pl. 3, fig. 10, 1817.
Lejeunia serpyllifolia Libert, Ann. Gen. Sci. Phys. **6**: 374, 1820 (not the *Jungermannia serpyllifolia* of Dickson, Pl. Crypt. Brit. **4**: 19, 1801).
Lejeunea serpyllifolia var. *cavifolia* Lindb., Acta Soc. Sci. Fenn. **10**: 485, 1875.
Lejeunea serpyllifolia var. *americana* Lindb., Acta Soc. Sci. Fenn. **10**: 486, 1875 (*p.p.*).
Lejeunea serpyllifolia Spruce, Trans. Bot. Soc. Edinburgh **15**: 262, 1884.
Eulejeunea serpyllifolia Schiffn., *in* Engler-Prantl, Nat. Pfl.-Fam. **1**(3): 122, 1895.
Lejeunea cavifolia Lindb., Acta Soc. Sci. Fenn. **10**: 43, 1871, *p. max. p.*; Evans, Mem. Torrey Bot. Club **8**(2): 151, 1902; Müller, Rabenh. Krypt.-Fl. **6**(2): 658, figs. 184, 185, 1916; Buch, Rev. Bryol. (n.s.) **7**: 240, figs. 3–4, 12–13; Frye and Clark, Univ. Wash. Publ. Biol. **6**(5): 795, 1947 (*p. p.*); Schuster and Hattori, Jour. Hattori Bot. Lab. No. **11**: 51, pl. XI, figs. 2–3, 1954.
Lejeunea cavifolia var. *planiuscula* Macvicar, Stud. Hdb. Brit. Hep. Ed. II: 431 (not of Lindberg, 1875).

In loosely attached, small, flat patches or tufts, or creeping over other bryophytes, a *clear to pale green* (more rarely distinctly yellowish or dark green), *dull* to quite shiny when dry. Shoots irregularly pinnately branched, the branches widely spreading; shoots *920–1200* (rarely to 1300)μ *wide* × 10–20 mm. long; stems 70–90 (100–110)μ in diam.; ventral cortical cells 23–38μ wide. Leaves *moderately imbricate, slightly to rather* strongly convex, obliquely to widely spreading (45–60°). Lobes oblong ovate, often slightly falcate, *widest clearly almost at the very base*, the arcuate, somewhat dilated antical base *extending across or slightly beyond the stem*, (the shingled dorsal lobes completely hiding the stem, in antical view), gradually rounded into the obtuse to rounded apex; postical margin, above keel, weakly arched to the apex; length of lobe usually 480–510 (rarely up to 600–650μ), its width (350) 370–390 (420)μ (*length usually 1.25–1.58 times the width*); margin essentially entire, the cells not bulging. Lobule large, nearly flat along free margin, but strongly inflated

[29] Although a high incidence of cladogynous inflorescences is the normal condition in *L. serpyllifolia*, occasional gatherings show a high incidence of acrogynous gynoecia, some of which may have gemminate innovations. A single such collection has been seen, from Carnedds, N. Wales (*Greig-Smith H 26*).

along the keel, its area *ca.* 1/9–1/6 (rarely to 1/4) of that of the dorsal lobe (on main stems); *lobule ca. 120–140μ wide × 160–180 (200)μ long, its length ca. 0.3–0.4 times that of dorsal lobe; keel moderately to strongly arched*, often gibbous, at its apex notched at juncture with free dorsal lobe (the angle between apex of keel and dorsal lobe usually 110–140°, exceptionally 90–100°); lobule with *apical cell blunt, little projecting*, the apex obliquely subtruncate, the sinus between apical cell and keel obsolete or shallow. Cells almost plane or slightly convex, pellucid, thin-walled, but *often with nodulose trigones and frequent intermediate thickenings*; marginal cells (18.5) 20–24 (26)μ near leaf-tips, in the lobe-middle becoming elongate hexagonal and up to 23–25 × 30–38μ but occasionally only 19–24 × 26–30μ (on leaves of branches); *oil-bodies (30) 40–50, occasionally up to 60 per cell, minute, homogeneous, fusiform to elliptical*, only 1.0–1.5 × 2–3μ up to 1.8–2 × 2.4–3μ, *highly glistening*, often persistent for years in herbarium material; chloroplasts larger than oil-bodies, 3.6–5μ long. Underleaves nearly *contiguous to subimbricate*, rarely slightly distant, *large, their area 2–3 (occasionally 4) times that of lobules*, rotundate to broadly ovate-orbicular, from slightly longer than wide to barely wider than long, widest at middle or slightly below middle, *bilobed* 1/5–3/5 (1/2), the sinus acute to rectangulate, rarely narrowly lunate; underleaves 200–255μ long × 180–250μ wide, occasionally 250–310μ long × 280–350μ wide, *their width usually 2.3–3 times that of stem*; lobes erect, triangular, acute to subacute, *usually 7–9 (10) cells wide at base*; bases of underleaves *somewhat cuneately narrowed* or narrowly rounded, *not cordate*.

Autoecious. Androecia usually on a short lateral branch; bracts in 2–4 pairs. *Female inflorescences most frequently on a leading branch*, occasionally on a short lateral branch; *always with 1 innovation*, the innovation sterile or soon again floriferous. Female *bracts large*, unequally bilobed and somewhat complicate; lobe suberect or obliquely spreading, more or less broadly obovate to oblong, 500–520μ long × 270–300μ wide, usually rounded to obtuse at the apex, the margins entire; lobule rather large, lingulate to lanceolate, rounded to longly acute at apex, free for 0.4–0.6 of its length, 300–400μ long × 90–110μ wide, entire-margined. Bracteole free or united for 0.1–0.2 of its length with one or both bracts, oblong to obovate, 400–450μ long × 200–215μ wide, bilobed 1/4–1/3, the erect lobes subacute or acute, triangular to ovate; sinus usually acute and narrow. Perianth *ca.* 800–850μ long × 400μ wide, exserted for *ca.* half its length, ellipsoidal-pyriform, *widest at or near middle*, the distal 1/2–2/5 sharply 5-carinate, the carinae not broadly dilated (the maximal width of the perianth at the middle: the distal half, including the carinae, not more extended laterally), suddenly narrowed distally, the perianth-apex truncate or rounded-truncate; keels smooth.

TYPE: Near Uppsala, Sweden.

DISTRIBUTION.—The "northernmost" of the species of *Lejeunea*, and the only one with a circumboreal distribution, ranging northward to 67°30′ (in Scandinavia) and up to 72° (in the Lena Valley, Siberia; *fide* Arnell; this is the only report from north of the Arctic Circle), but in North America not known north of the 50° of Latitude. The species is also our only one which is widespread at rather high elevations (up to 2500 meters, perhaps higher, in Europe), although *L. lamacerina* ascends to 1800–2200 meters in the Southern Appalachians. Southward, the species extends to Tunis and the Canaries (south to *ca.* 28° Latitude), but in North America occurring southward, in the mountains, only to *ca.* 35°30′ N. Latitude.[30] In North America from the southern edge of the Coniferous Forest to the Mixed Mesophytic Forest.

[30] The recent reports of the species from as far south as Dade Co., Florida, southern Louisiana, and Mississippi, in Frye and Clark (1947), represent misdeterminations for the unrelated *L. flava*. Similarly, the reports of the species from Dade, DeSoto, Glades, Hardee and Polk Cos., Florida (Redfearn, 1952) also represent misdeterminations. I have seen

The species occurs nearly throughout southern and central Europe, occurring from northern Africa (Tunis and Algeria!) northward through Spain (Buch, 1934) and from Dalmatia, Portugal, the Balearic Isls., and Italy, to England and Ireland, northward to Scandinavia (Sweden, *type*; Norway; Finland), eastward into Russia, and into Siberia (Lena R. Valley, Bulkur [= Bulun], *teste* Arnell); also southeastward to the Black Sea (Trapezunt) and to the Caucasus. Also reported from Japan. In the Atlantic Ocean going southward to the Azores (Allorge, 1950) and to the Canary Islands.

In North America with a Eury-Appalachian distribution, extending from Quebec to the Southern Appalachians, westward to the Great Lakes area of Minnesota and Ontario, as follows:

CANADA. **Quebec:** St. Anne-des-Monts R., Gaspé (On *Thuja;* Macoun, 1902); La Tuque; Pont Rouge; Bic; Mt. Shefford (Lepage, 1945; Fabius, 1950). **Nova Scotia:** Sandy Cove (Lowe, 1909); Barrasois and Cape Smoky, Cape Breton I. (Nichols); Port Mouton (Brown, 1936); Sandy Cove, Digby (*M. S. Brown 253!*). **Miquelon I.** (Macoun, 1902). **Newfoundland:** South Branch, Steady Brook, Benoit Brook, all in W. Nfld.; Norris Arm, in N. C. Nfld. (Buch and Tuomikoski, 1955). **Ontario:** Belleville; Algonquin Park; York Co. (Macoun, 1902). UNITED STATES. **Maine:** Mt. Desert I. (Lorenz); Greenville (Evans, 1912). **New Hampshire:** Franconia Mts. (Lorenz, 1908; also Evans, 1903), Grafton Co. (Grafton, *Hutchinson 1949!*). **Vermont** and **Rhode Island:** (Evans, 1913). **Massachusetts:** Mt. Greylock (Andrews, 1909). **Connecticut:** Litchfield, Fairfield, New Haven and Middlesex Cos. **New York:** Herkimer Co. (Haynes); Tompkins, Cortland, Onondaga, Madison, Schuyler, Steuben, Allegany, Ontario, Genessee, Cattaraugus Cos. (Schuster, 1949). **Pennsylvania:** Alleghany, Bedford, Huntington, Lawrence, McKean Cos. (Lanfear). **West Virginia:** Monongalia, Nicolas, Pocahontas, Preston Cos. (Ammons, 1940); w. of mouth of Seneca, Monongahela Natl. Forest (*Schuster 18300c, 18308*); w. slope of Shenandoah Mt., e. of Brandywine (*Schuster 18382, 18373, 18384*). **Virginia:** GILES CO. (Mt. Lake, Patterson, 1949); RAPPAHANNOCK CO. (Patterson, 1949; Buck Hollow Trail, 1500–3000 ft., *Schnooberger 4538;* reported by Schnooberger and Wynne, 1945, as "*L. patens*"); PAGE CO. (Appalachian Trail between Crescent Rocks and Franklin Cliffs, 3000–3500 ft., *Schnooberger 4786b*). **North Carolina:** ASHE CO. (Bluff Mt., *ca.* 4600 ft., near W. Jefferson, *Schuster 29548;* plate); POLK CO. (Melrose Falls, n.w. of Tryon, *Schuster 36045;* southernmost report, at *ca.* 35°30′ N.). **Tennessee:** Hamilton and Sevier Cos. (Sharp, 1939).[31] Westward to: **Michigan:** ONTONAGON CO. (Agate Falls, *Nichols and Steere*, Aug. 1935); KEWEENAW CO. (Summit of Mt. Bohemia,

seven specimens from Florida (Polk, DeSoto and Hardee Cos.) determined by Redfearn, and forming part of the basis for the reports of the species from Florida in Redfearn (1952), six of them contain at least some *Lejeunea flava*, and no other species of this subgenus; the seventh contains only *Cheilolejeunea rigidula*.

[31] Dr. A. J. Sharp kindly loaned the writer the Tennessee collection of *Lejeunea*. I could find only three packets, assigned to *L. cavifolia*, all from Rutherford Co. and all from the same locality (Snail Shell Cave near Murfreesboro), *Bold 21* (1939), *Bold and Sharp 34310* (1934), and *Bold 4* (1934). Two of these packets were annotated by Morrison in 1937, and served as the basis of part of the report of *L. cavifolia* from Tennessee in Morrison (1938).

This material, however, is identical with the plant, from the same locality, referred by both Morrison (1938) and Sharp (1939) to *L. glaucescens*. As discussed under that species subsequently, these plants fail to show any close affinity with either *L. glaucescens*, or with *L. cavifolia*. The material reported as *L. glaucescens* represents a more robust phase of the same plant; it shows preponderantly cladogynous perianths. The plants reported as *L. cavifolia* (*Bold 4*, 1934) are very poorly preserved, and sparing. They show numerous cladogynous gynoecia, but I could find no acrogynous ones.

Steere, Sept. 1936; Ft. Wilkins, *Steere*, 1935; Ryan Isl., Siskowit Lake, Isle Royale, *Povah et al. 343;* Phoenix, *Steere*, 1936); CHEBOYGAN CO. (n. of Burt Lake, *Steere*, Aug. 1940); MACKINAC CO. (Bois Blanc I., *Wynne 2570*); MARQUETTE CO. (Sugar Loaf Mt., Marquette, *Steere*, Aug. 1936; Mountain Stream, Huron Mts., *Nichols 235*); ONTONAGON CO. (Rd. to Nonsuch Mine, *Nichols and Steere*, Aug. 1935; Agate Falls, *Nichols and Steere*, Aug. 1935); EATON CO. (near Grand Ledge, *Steere 457*); LEELANEAU CO. (Glen Lake, *Darlington 213*); CHIPPEWA CO. (Sugar I., *Steere 3475*); ALGER CO. (Miners Falls, near Munising, *Conklin*, 1937). **Wisconsin:** LINCOLN CO. (Grandmother Bull Falls, Conklin, 1929); IRON CO. (Montreal R., Conklin, 1929). **Minnesota:** Carlton, Cook, Itasca, Lake and St. Louis Cos. (Schuster, 1953).

Lejeunea cavifolia extends further northward than any other regional member of the family. It and *L. lamacerina* are our only species of *Lejeunea* restricted to the non-coastal plain portions of the continent.

ECOLOGY.—Occurring under a diversity of conditions, as an epiphyte on bark (of deciduous trees, such as *Populus tacamahaca* and *Betula lutea*; northward also occasionally on *Tsuga canadensis*, more frequently on the bark of *Thuja occidentalis*), both on the bole of trees, and on exposed roots; more rarely on stumps; frequently on shaded rocks.

On the bark of trees frequently associated with *Cololejeunea biddlecomiae*, *Metzgeria furcata* and *conjugata*, *Radula complanata* and *obconica*, occasionally with *Frullania eboracensis*, *bolanderi*, and *oakesiana*. It usually occurs on trees only in areas with a high humidity, such as swamps, bogs, or deep ravines.

On rocks, the species occurs under a wide diversity of conditions, both on acidic rocks and occasionally on basic rocks, such as shales and sandstones, occasionally over limestone. It is found here chiefly on shaded ledges and boulders, associated with *Radula obconica* and *complanata*, *Porella platyphylla*, *Metzgeria conjugata*, *crassipilis*, and *furcata*, occasionally also *Frullania asagrayana* or *tamarisci*, *Cololejeunea biddlecomiae*, *Lophocolea bicuspidata*, *Scapania nemorosa*, *Plagiochila asplenioides*. At the northern edge of its range (in Minnesota), it may occur over basalts with *Scapania gymnostomophila* and *Cephaloziella hampeana*. Relatively rarely the species may invade marly soil.

Both on rocks and on bark the species is clearly a pioneer, generally a member of the more mesophytic facies of the *Lejeunea-Frullania-Radula* Associule. "It invades bare, unprepared rock faces where the sun is not too direct. . . . With the development of any amount of soil, the species is soon succeeded by other, more mesic forms" (Schuster, 1953). Although the species is generally considered an oxylophyte, Müller (1916, p. 660) stating that it occurs "vor allem auf Silikatgestein . . .," the distribution in the northeastern United States suggests that it has a high tolerance for calcareous conditions. It is, for instance, reported from the "moist shaded sides of large limestone boulders. . ." and from "shaded, calcareous sandstone ledges" in Michigan. Schuster (1953), discussing its distribution in Minnesota states, "Though not a pronounced calciphile, the species may be somewhat restricted by the dependency on at least traces of lime . . .", while it is reported in New York as associated, on moist ravine-walls, with such calciphiles as *Lophozia badensis* and *Cololejeunea biddlecomiae* (Schuster, 1949). The frequent occurrence on the bark of the calciphilous *Thuja occidentalis* is also

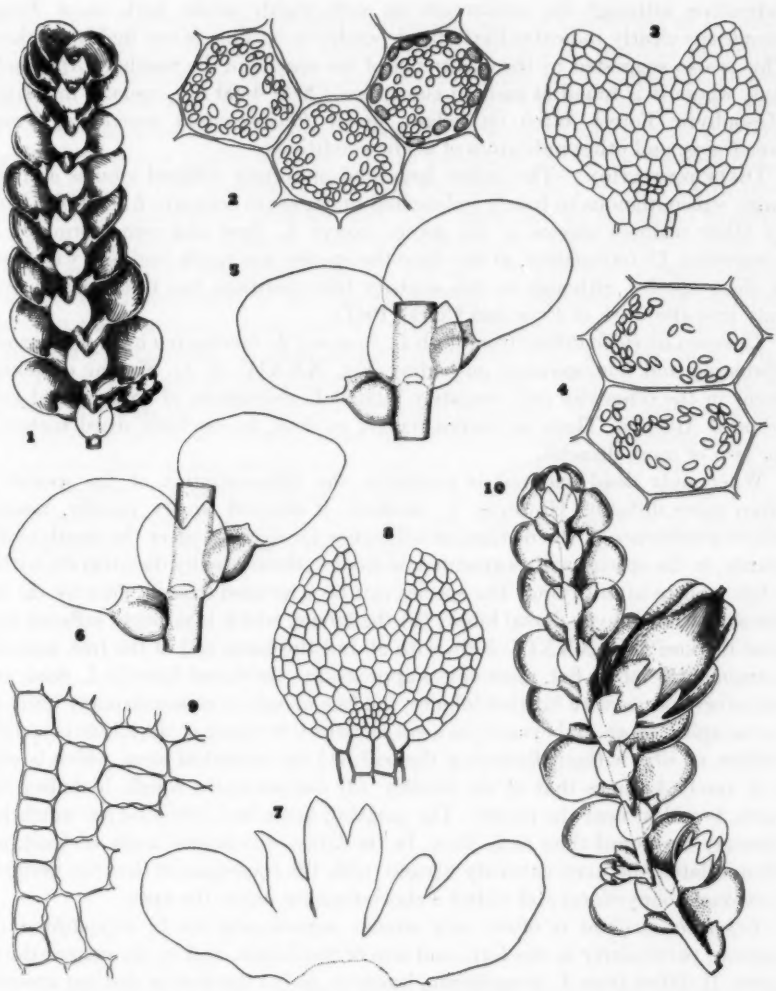

FIG. XXXIV. *Lejeunea cavifolia* (Ehrh.) Lindbg. 1. Sterile shoot, postical aspect (×25); 2. Median cells with oil-bodies, the cell at right also with chloroplasts stippled in (×620); 3. Underleaf (×132); 4. Two cells, leptodermous phase, with oil-bodies (×820); 5–6. Postical aspect of shoot-sector (×55); 7. Ring of bracts and bracteole (×55); 8. Underleaf (×100); 9. Marginal cells near leaf apex (×275); 10. Fertile shoot, with single innovation (×25). (Figs. 1, Ithaca, N. Y., *Schuster*; 2, *Schuster 18300c*, West Virginia; 3–7, *Schuster 29548*, near Tryon, North Carolina; 8–9, *Schuster 13441*, Minnesota; 10. Turkey Run State Park, Ind., *Schuster*.)

indicative, although the occurrence on such highly acidic bark as of *Tsuga canadensis* clearly indicates that any dependency on lime is not highly marked. This is also suggested by the occurrence of the species in the Southern Appalachians, where it is found at median elevations (2000–4500 ft.), usually in Mixed Mesophytic Forest, often on ledges, under *Rhododendron maximum*, *Tsuga canadensis*, and other indicators of acidic conditions.

DIFFERENTIATION.—The rather large and uniformly inflated lobules and the large, subcontiguous to barely imbricated underleaves separate *L. cavifolia* from all other regional species of the genus, except *L. flava* and some forms of *L. lamacerina*. Unfortunately, at one time the species was much confused with both of these species, although in this century this confusion has been carried over only into the work of Frye and Clark (1947).

Lejeunea cavifolia differs from both *L. flava* and *L. lamacerina* in the numerous, glistening and homogeneous oil-bodies (Fig. XXXIV: 2, 4). Similar oil-bodies occur in the otherwise only remotely related *L. minutiloba* of tropical and subtropical America. These oil-bodies remain evident, in carefully dried material, for two or more decades.

When only dead material is available, the differentiation of the species is often more difficult. However, *L. cavifolia*, if allowed to dry rapidly, usually shows persistence of the distinctive oil-bodies for decades after the death of the plants; in the species with segmented oil-bodies, these usually disintegrate within a few months after drying. The species can be separated from *L. flava* by (a) the the somewhat convex dorsal lobes; (b) the lobule, which is strongly inflated only near the keel (Fig. XXXIV: 5–6), with all but the basal end of the free, anterior margin of the lobule flat, more or less appressed to the dorsal lobe (in *L. flava*, and our other species with inflated lobules, the free margin is rather strongly involute to the apical tooth, or beyond); as a consequence, the apex of the lobule is usually visible, *in situ*, without flattening the leaf; (c) the underleaf area, which is only 2–3, rarely 4, times that of the lobules; (d) the perianth, which, including the keels, is widest near the middle. The perianth keels in *L. cavifolia* are much less strongly developed than in *L. flava*. In the latter, the lateral keels, at least, are often dilated and even narrowly winged, with the consequence that the perianth is strongly obpyriform and widest a short distance below the apex.

Lejeunea cavifolia is often very similar superficially to *L. serpyllifolia* (= *patens*), particularly in the form and size of the lobule, and in the convex dorsal lobes. It differs from *L. serpyllifolia*, however, in (a) the lack of distinct crenulation of the leaf and underleaf-margins (Fig. XXXIV: 9); (b) the somewhat smaller lobules, never as much as 0.45–0.55 of the length of the dorsal lobes; (c) the larger underleaves; those of *L. serpyllifolia* are not distinctly larger than the lobules; (d) the usually less arched keel, with the postical margin less indented at juncture of keel and dorsal lobe (Fig. XXXIV: 5–6); (e) the perianth-form; that of *L. serpyllifolia* agrees with that of *L. flava* in being widest well above the middle.

Lejeunea cavifolia was at one time much confused with the plant lately separated by Buch (1934) as *L. planiuscula* (Lindb.) Buch. Recent work (Greig-

Smith, 1954; Persson, 1939) has shown that the latter is a synonym of *L. lamacerina* Gottsche *ex* Stephani. *L. lamacerina* differs from *L. cavifolia* in having segmented oil-bodies (i.e. of the *L. flava* type). It does not appear to be closely related to *L. cavifolia*. The statement, in Frye and Clark, 1947, p. 798, that, "From our examination of American material we were led to conclude that the variety *planiuscula* grades into the species [*cavifolia*] and should be dropped," has no validity. This is evident when one considers that Frye and Clark misdetermined *L. flava* for *L. cavifolia*, and could have seen no transition between *L. planiuscula* and *L. cavifolia*, since the former was not known to occur in North America until 1955 (Buch and Tuomikoski). In addition to the profound difference in oil-body form, *L. cavifolia* differs from *L. lamacerina* in the perianth shape; in the commonly more narrowly ovate-oblong leaf lobes; in the larger, more nearly contiguous or overlapping underleaves with broader lobes (Fig. XXXIV: 1, 10); and in the slightly larger leaf cells. Admittedly, with dead material in which the oil-bodies are no longer preserved, the separation of the two species is at times difficult, since superficially transitional phases are not uncommon. Mature underleaves in *L. cavifolia* are more shallowly bilobed than in *L. lamacerina*, the sinus descending commonly only to within 4–6 cells of the rhizoid-initial region (Fig. XXXIV: 3, 8); also, the lobes tend to be broader, often ranging up to 8–10 cells wide at base.

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Department of Botany
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(5) BRAUER, A., AND N. MACON. Amer. Jour. Math. **71**: 349–361. 1949.
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FERNALD, M. L. 1950. Gray's Manual of Botany, 8th ed. American Book Company.

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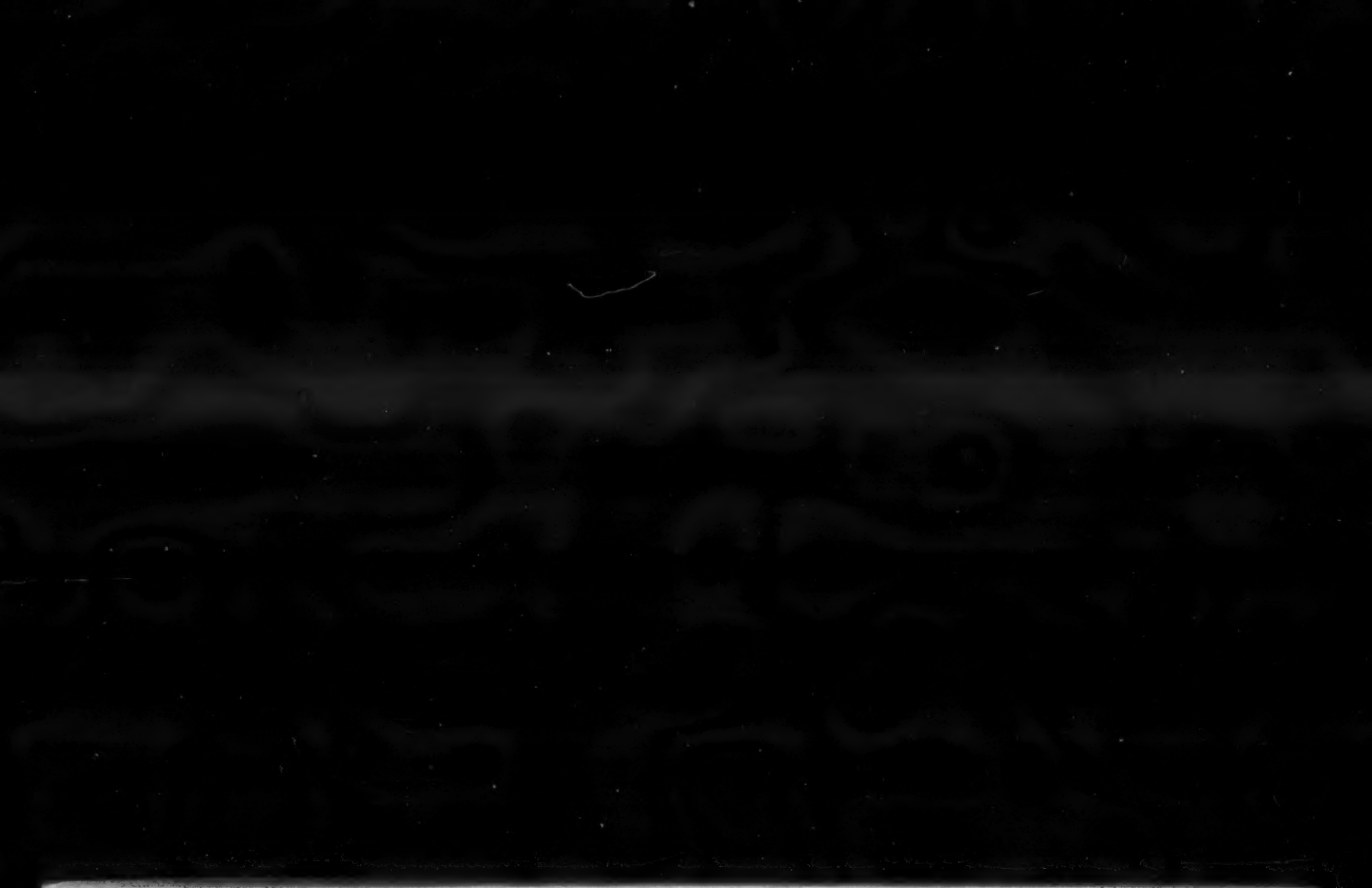
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